THE

TAXONOMY, PHYLOGENY AND BIOGEOGRAPHY

OF THE MARROLITHINAE

(TRINUCLEIDAE, Trilobita)

By

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(PhD Thesis)

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Abstract:

Trinucleid trilobites are characterised by their pitted fringes on the cephalon. The Marrolithinae is a subfamily of the Trinucleidae in which the innermost arc of pits is truncated by the next arc and flange pits are present along the posterior to posterolateral edge of the genal lobe. The Marrolithinae currently comprise ten genera and some 60 species and subspecies and had its origins on the margin of Gondwana during the rifting and northward drift of numerous microplates during the mid Ordovician. The history of the Marrolithinae reflects a complex, but currently unresolved, pattern of migration back and forth across the widening gulf of the Rheic Ocean from the early Llanvirn until the mid Ashgill such that species are now found in the Anglo-Welsh area, France, Iberia, Bohemia, Turkey, Central Asia, N. Africa and part of S. America. The Marrolithinae are widely used for European, North African and Turkish correlation and are zonal indicators for several Anglo-Welsh biozones.

An extensive and detailed overhaul of the present classification of the Marrolithinae is undertaken to produce a clear taxonomic framework from which to understand the phylogeny and biogeographical history of the subfamily. Historically, marrolithine species have been defined using a strongly typological approach which has increasingly proved unworkable as species show ranges of variation in morphology that have led to uncertainty in the identification of specimens and has therefore lowered their stratigraphical usefulness. The lack of appreciation of morphological variation has resulted in the naming of a great many more species than are probably actually present in the fossil record. Extensive museum collections have been analysed supplemented by field sampling within Wales and Shropshire and comparison of field locations and horizons. A large collection of over 2000 specimens of Llanvirn to Ashgill Moroccan Marrolithinae was studied for the first time. This material has been important in the reclassification of the Marrolithinae. These samples contain the earliest *Onnia* specimens and have therefore thrown light on the *Deanaspis* and *Onnia* lineage as presently understood. The Moroccan samples also contain the earliest representatives of the new genus *Hammannaspis*. The Moroccan species played an important role in the distribution of the Marrolithinae around proto-Tethys.

The re-evaluation of the classification of marrolithine genera and species has included the first cladistic analysis of a trinucleid subfamily, detailed analysis of variation in fringe pit

development within samples and taxa and consideration of the palaeogeographical relationships between the marrolithine taxa in space and time. These differing approaches have led to the production of a more constrained and easier to use classification which will enhance the stratigraphical usefulness of the Marrolithinae.

The Marrolithinae as revised herein comprises 30 species and subspecies within the genera *Marrolithus* [within which *Costonia* is synonymized], *Protolloydolithus, Reuscholithus, Bettonolithus, Whittardolithus, Lloydolithus, Marrolithoides, Deanaspis, Onnia* and *Hammannaspis* gen. nov.

The ancestor of *Protolloydolithus* is undoubtedly the Hanchungolithinae, *Hanchungolithus*. *Bettonolithus* probably gave rise to three stocks: *Whittardolithus* and *Lloydolithus* as one stock and *Marrolithus* and *Hammannaspis* gen. nov. as another. *Reuscholithus* was probably a derivative the one of the youngest *Marrolithus* species. *Marrolithoides* was most likely the Anglo-Welsh representative of *Hammannaspis* gen. nov., a genus that did not appear in Avalonia. *Deanaspis* and *Onnia* coexisted early in the Caradoc and make up the third *Bettonolithus* stock.

Recognition of variation between samples of what are now recognised as the same species has important implications on the previous typological approach to the taxonomic classification of the Marrolithinae. These variations include the temporal and spatial changes in the extent and elevation of fringe inflations in *Marrolithus favus favus, M.* (s. l.) *elegans* and *M.* (s. l.) *arenarius.* Using the revised taxonomy the palaeogeographical history of the subfamily becomes clearer. The main migration directions for the marrolithines appears to be contrary to ocean currents of the Arenig as presently understood. The complex migration around the peri-Gondwanan margin also sheds light on the relative positions of the Perunican, Armorican and Iberian microplates.

Acknowledgements

I would like to thank my two supervisors Alan Owen and Keith Ingham for their guidance and unending patience. I also thank the curatorial staff at all the museums and other institutions visited, with special thanks to Bob Owens, Derek Siveter, Andy Ross, Mike Dorling Steve Tunicliffe Euan Clarkson and Mike Jewkes. Thanks also to Pete Sheldon and Adrian Rushton for their words of encouragement. NERC and my husband, Simon, for financial support. Mum and Dad and all my family and friends for the help.

To the loving patience and kindness of my son, Calum, this is for you.

Declaration

The material presented in this thesis summarises the results of three years of research carried out in the Division of Earth Sciences of Glasgow University under the supervision of Drs A. W. Owen and J. K. Ingham. This study is based on my own independent research and any previously published or unpublished results of other researchers used in this thesis have been given full acknowledgement in the text.

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1 INTRODUCTION

Trinucleid trilobites are characterised by their pitted fringes on the cephalon. The Marrolithinae is a subfamily of the Trinucleidae in which the innermost arc of pits is truncated by the next arc and flange pits are present along the posterior to posterolateral edge of the genal lobe. The Marrolithinae currently comprises ten genera and some 60 species and subspecies and had its origins on the margin of Gondwana during the rifting and northward drift of numerous microplates during the mid Ordovician. The history of the Marrolithinae reflects a complex, but currently unresolved, pattern of migration back and forth across the widening gulf of the Rheic Ocean from the early Llanvirn until the mid Ashgill such that species are now found in the Anglo-Welsh area, France, Iberia, Bohemia, Turkey, Central Asia, N. Africa and part of S. America.

1.1 Aims

The aims of this project are to produce an extensive and detailed overhaul of the present classification of the Marrolithinae to establish a clear taxonomic framework from which to understand the phylogeny and biogeographical history of the subfamily. Historically, marrolithine species have been defined using a strongly typological approach which has increasingly proved unworkable as species show ranges of variation in morphology that have led to uncertainty in the identification of specimens and has therefore lowered their stratigraphical usefulness. The lack of appreciation of morphological variation has resulted in the naming of a great many more species than are probably actually present in the fossil record. Some previous workers have revised and synonymised species but this has not been attempted comprehensively for the whole subfamily. The Marrolithinae are widely used for European, North African and Turkish correlation and are zonal indicators for several Anglo-Welsh biozones.

1.2 Historical review

The extensive literature on the Trinucleidae began in the early nineteenth century; the systematic descriptions of new species in some instances was also accompanied by discussions on morphology, distribution and ontogeny. *Trinucleus ornatus* Sternberg, 1833 was the earliest description of a species now assigned to the Subfamily Marrolithinae. Murchison followed with his description of *Trinucleus Lloydi* in 1839. Barrande a few years later (1846) described *Trinucleus goldfussii*. The following year, 1847, Salter, Rouault and Hawle and Corda described the species *Trinucleus favus*, *Trinucleus pongerardi* and *Trinucleus senftenbergii* respectively with Hawle and Corda erecting the Family Trinucleidae. Salter (1848) began to see very close similarities between some trinucleids with his species designation of *Trinucleus ornatus* var. *favus*. Barrande in 1852, Hicks in 1875 and Bergeron in 1894 described *Trinucleus ultima*, *Trinucleus ramsayi* and *Trinucleus grenieri*. In 1895 Oehlert described both *Trinucleus bureaui* and *Trinucleus maladai* with Kerforne in 1900 introducing *Trinucleus suenesi*.

Bancroft (1929) was the first to detail the importance of using pitted fringes for trinucleid classification. He erected the genera *Marrolithus* and *Reuscholithus* and described *R. reuschi*, *Cryptolithus cobboldi*, *C. gracilis*, and *C. superbus*; detailing fringe and pit morphology and distribution. By 1940 other workers were beginning to see the importance of the pitted fringes and built on Bancroft's original work. Over the next 20 years, Williams (1948), Whittington and Williams (1955) and Whittington (1966) all in Wales, Whittard (1956, 1958) in the Shelve Inlier and Dean (1960) in South Shropshire were some of the most prolific namers of new species of marrolithines. By 1960 the genera *Marrolithus* Bancroft, 1929*b*, *Reuscholithus* Bancroft, 1929*b*, *Onnia* Bancroft, 1933, *Lloydolithus* Bancroft, 1933, *Bettonia* Whittard, 1956, *Marrolithoides* Williams, 1948, *Costonia* Dean, 1960 and *Protolloydolithus* Williams, 1948 were established. Classification was still very typological with strict definitions based on pit numbers and patterns, leading to many workers showing uncertainty in their assignment of specimens to species.

Hughes (1970) reviewed the notation and methods of presentation for trinucleid fringe pit data. A year later he erected the subfamily Marrolithinae for genera closely related to *Marrolithus* but which were previously placed in the Cryptolithinae, namely *Marrolithus*, *Marrolithoides*, *Protolloydolithus*, *Reuscholithus* and *Costonia*. However, Hughes left

Bettonia within the Cryptolithinae. An important point discussed by Hughes was that pit distribution and the number of pits per arc are not dependant on the size of the individual. The fringe assumes its final characteristics very early on in meraspid stage development (see also Whittington, 1941 and 1959).

A greater appreciation of the role of pit distribution in trinucleid classification led Hughes, Ingham and Addison to produce a review of the entire Trinucleidae in 1975. They summarised, and partly established, the modern morphological and taxonomic framework for the Trinucleidae including the establishment of Marrolithinae genera *Deanaspis* and *Whittardolithus*.

Morris (1988) produced a summary of all British trilobite species and reallocated the species formerly placed in *Bettonia* to a new genus *Bettonolithus* as the former name was preoccupied. Owen and Ingham (1988) gave detailed pit distribution and statistical data for successive population samples of *Onnia* from the Onnian of Shropshire where three successive biozones based on species or subspecies of the genus are recognised.

Shaw (1995) discussed the Bohemian Marrolithinae including species of *Deanaspis*. He raised concern over the difficulties of distinguishing between *Onnia* and *Deanaspis*; closely related genera distinguished by differences in fringe girder and pseudogirder development. Hammann and Leone (1997) described specimens from southern Sardinia and described two distinct morphological groups with what they interpreted as *Deanaspis*, distinguished by their glabella shape, convexity of genal lobes, steepness of fringe and girder and pit characters.

Bettley *et al.* (2001) used marrolithine species amongst other faunal elements to revise the standard British biozones through the Llandeilian-Caradoc interval.

1.3 Material

The extensive museum collections of Marrolithinae from the Hunterian, Natural History and Sedgwick museums, National Museum of Wales, Oxford and Birmingham universities and British Geological Survey have been analysed, with up to 50 separate items of information

from each cephalon being collected. Some field sampling within Wales and Shropshire and comparison of field locations and horizons was also undertaken

As part of this research, a large collection of over 2000 specimens of Llanvirn to Ashgill Moroccan Marrolithinae was studied for the first time. They were collected during the 1960's by Dr Jacques Destombes as part of an international project on the Palaeozoic geology of Morocco which culminated with the publication of "Lower Palaeozoic Rocks of the World, Volume 4" (Holland 1985). The Marrolithinae, as well as other parts of the fauna, was left undescribed. This material is of immense value as the sampling was stratigraphically well constrained and the taxa present have an important bearing on some of the taxonomic problems within the subfamily.

1.4 Methods

Several methods were employed to re-evaluate the classification of Marrolithine genera and species during this study. These included the first cladistic analysis of a trinucleid subfamily. Detailed analysis of variation in fringe pit development within samples and taxa was used to provide workable diagnoses of species and genera. Palaeogeographical relationships have also been studied with the production of detailed distribution maps for the separate Ordovician stages to better understand the relationships between the marrolithine taxa in space and time. These differing approaches have led to the production of a more constrained and easier to use classification which will enhance the stratigraphical usefulness of the Marrolithinae.

Digital photography was used to aid data collection and facilitate morphological comparisons. Specimens to be photographed were prepared, cleaned, darkened using photographic opaque and then whitened using the smoke from burning magnesium ribbon. A digital camera set-up was used for photography with a Kodak Digital Science Professional DCS 410c digital camera unit (equivalent to ISO 100) attached to the back of a Nikon FM2 camera body. A 55mm lens and combinations of extension rings were attached to obtain the required magnification. The basic set up follows that of Siveter (1990) using a similar Leitz Aristophot stand and a 30cm diameter, 32-watt ring light. To obtain the necessary NW light direction a moveable cover was made to fit on the ring light to cover the SE corner. The image size of 1524 x 1012 pixel (13.8 x 9.2mm) was transferred from the camera into Adobe

Photoshop. The photographs were then reduced to grey scale, cropped, saved as JPEG files and finally burned onto a CD. The photographs were then transferred into PowerPoint or Photoshop / Corel Photo for final processing. All photographic plates were produced electronically.

1.5 Layout of the thesis.

The layout of this thesis is somewhat different from the standard arrangement of having the systematics section towards the end of the volume. The Morphology Chapter outlines the general morphology of the trinucleid trilobites and the Marrolithinae, in particular. It is followed by a chapter describing the cladistic analysis of the subfamily within which the present classification is assessed based largely on the genera and species as currently understood. The classification advocated herein is highlighted near the end of the chapter. The Systematics Chapter has been placed next so the reader is introduced to the new classification which involves considerable synonymy of named species, the emended diagnosis of most genera and the establishment of a new genus. This provides the necessary precursor to the consideration of the spatial and temporal distributions of marrolithine taxa discussed in the subsequent chapters.

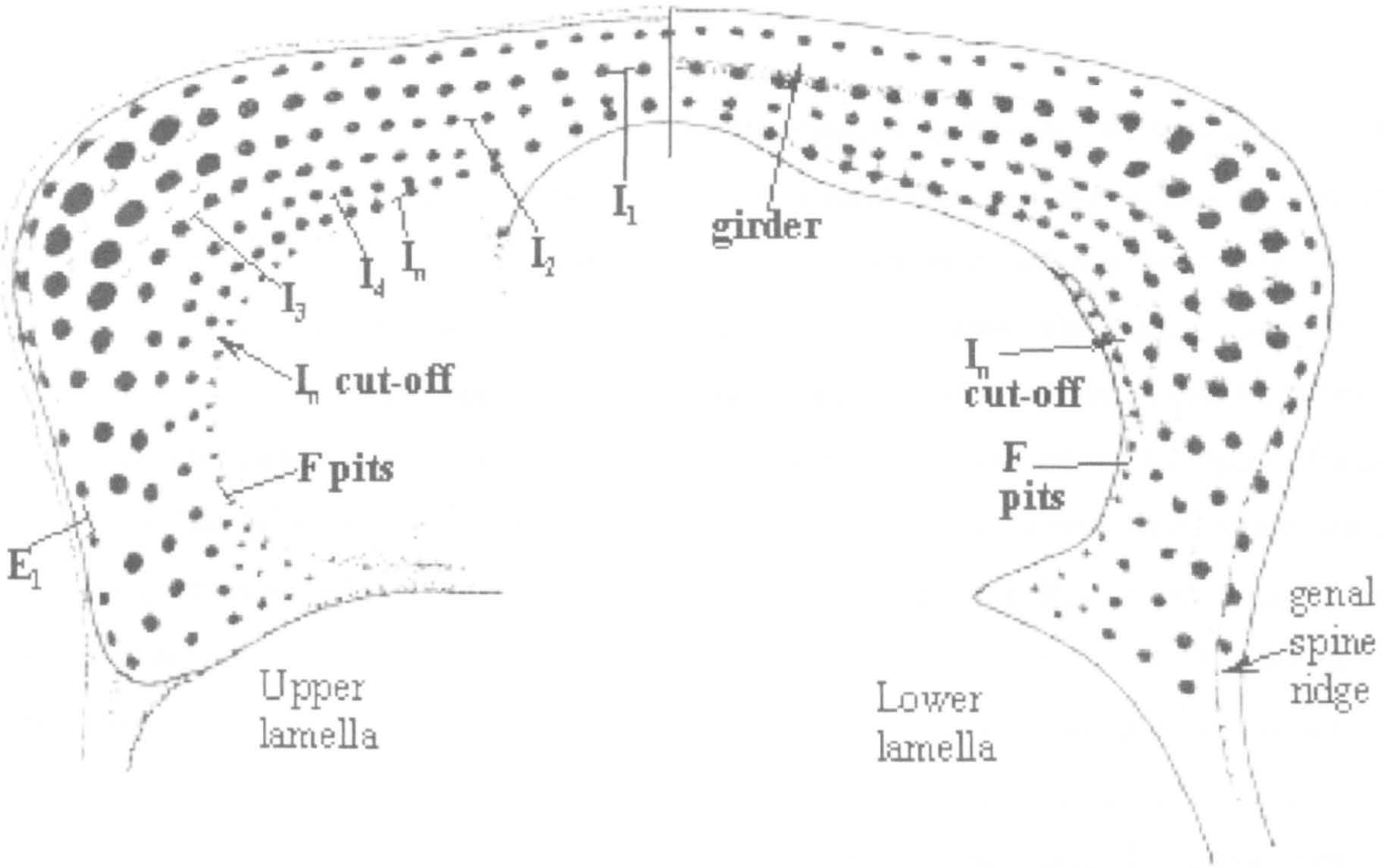
2 MORPHOLOGY

2.1 The Morphology of Trinucleidae.

Hughes *et al.* (1975) summarised, and partly established, the modern morphological and taxonomic framework for the Trinucleidae. One of the characteristic features of the family is the presence of a bilamellar cephalic fringe bearing an array of funnel shaped pits of presumed sensory function (see Chatterton 1980, p. 6). Although the early representatives of the family have an irregular fringe pit distribution, most of the later forms show various patterns of regular arrangement of the majority of the pits into concentric arcs and radial rows. The notation applied to the fringe pits is summarised on Text-Fig. 2.1 and follows that advocated by Hughes *et al.* (1975), based on Bancroft (1929*b*) and subsequent modifications, including those of Ingham (1970).

2.1.1 Morphological terminology.

The classification of trinucleid trilobites is based almost entirely on the distinctive features of the pitted, fringed cephalon. The thorax and pygidium are very similar throughout the family and are of limited use taxonomically. During ecdysis the marginal suture separated the long genal spines and lower lamella from the upper lamella, glabella and genal lobes. On the ventral surface of the lower lamella, the elevated ridge confluent with the pronounced ventral ridge on the genal spines is termed the girder and all other ventral ridges are termed pseudogirders. In some species narrow ridges or lists are present on the upper lamella positioned above one or more of the ventral ridges. The position of the arcs in relation to the girder on the lower lamella is the basis for the fringe notation with arcs external to the girder termed E arcs and those internal to it, I arcs. The innermost (and ontogenetically earliest) I arc is termed I_n, the other arcs are numbered, sequentially, away from the girder as shown in Text-fig. 2.1.



Text-Fig. 2.1 Sketch of *Marrolithus f. favus* (Salter) showing upper and lower lamellae and terms used.

Inner arc radial rows are produced when the pits in adjacent arcs are aligned. These are numbered sequentially away from the sagittal line; the first radial row is termed R0 if it lies on the sagittal line or R1 if adjacent to it. The two sides of the fringe are numbered separately, sharing only the median row (R0) if it is present. Flange pits (F pits) lie between I_n or the adjacent I arc in the Marrolithinae and the posterolateral parts of the genal lobes, and are much smaller than the other pits. On the lower lamella they occupy the flange – its bevelled innermost position accomodates the thoracic segment tips on enrollment. F pits are only present in the Cryptolithinae and the Marrolithinae. Some genera (e.g. *Lloydolithus*) have numerous small irregular pits posteriorly that can be difficult to distinguish from F pits when viewed on the upper lamella; they can however, be readily identified on the lower lamella. Posterior margin pits (PM pits) lie along the posterior margin of the cephalon and may include F, I and E pits. A key feature of the Marrolithinae is that the I_n arc is terminated - "cut off"- by an adjacent I arc before the posterior margin is reached.

In addition to the recognition of the number of I and E arcs and the other features noted above, the number of pits on a given arc, expressed as a half-fringe value, has been an important diagnostic criterion in trinucleid taxonomy (e.g. Whittington 1968, p. 704) and many trinucleid species have been diagnosed on the basis of half or incomplete fringe

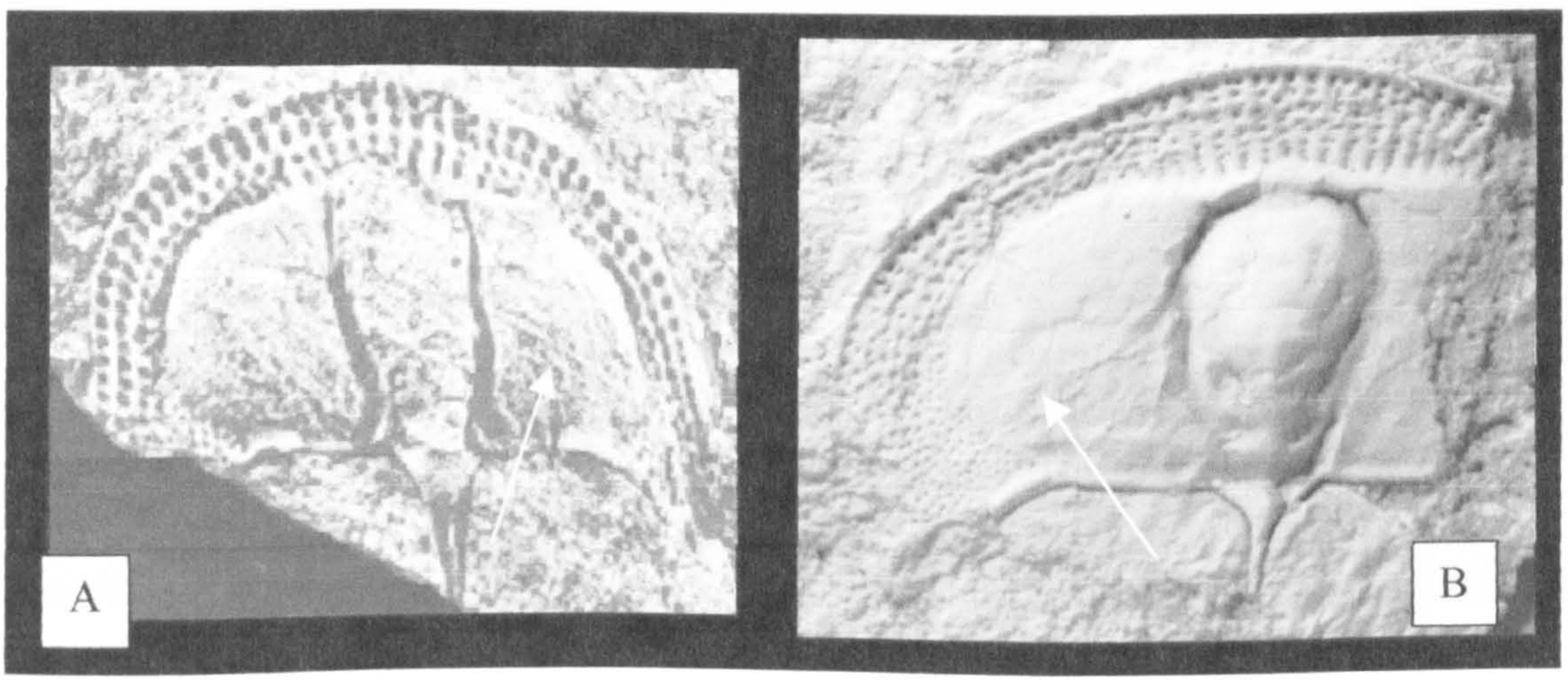
descriptions. Using large samples of *Trinucleus fimbriatus* Murchison, 1839, Hughes (1970) addressed the problem of fringe symmetry. He concluded that: operator errors in selecting half-fringes were negligible, major features of the pit distribution are not dependent on the size of specimen for late meraspid or younger individuals (see also Whittington 1941, 1959) and there are no statistically significant differences between the left and right half-fringes within a sample, although individuals commonly exhibit some asymmetry. Complete fringes of specimens belonging to the Marrolithinae in the present study invariably show some degree (usually two or three pits) of asymmetry in all arcs and the same applies to the Anglo-Welsh Cryptolithinae (see Bowdler-Hicks *et al.*, 2002). Thus three subfamilies: Marrolithinae, Cryptolithinae and Trinucleinae suggest that fringe asymmetry is ubiquitous within the Trinucleidae. The median line can lie along a radial row of pits, a radial ridge or a combination of both ridges and pits in different arcs. Pits that lie along the median line are counted as half a pit. Misidentification of the median line could lead to an apparent asymmetry of one or two pits but generally this would still keep the specimen within the normal range of variation of pit counts.

The types of asymmetry noted above should not be confused with that of abnormal fringes which may have arisen through repair of an injury, teratology (genetic or embryological malfunction) or pathological conditions (disease or parasitic infestation) (see Owen, 1983, 1985 for more details). However, these types of asymmetries may occasionally go undetected, because of advanced repair of an injury or minor teratological or pathological conditions.

Throughout the Marrolithinae, and Trinucleidae as a whole, the thorax, containing six tagmata in the holaspis stage, shows little morphological variation. The pygidium is sub-triangular, with axial rings and pleural ribs becoming indistinct posteriorly. Sheldon (1987) analysed several trilobite taxa including the trinucleid *Whittardolithus* in the upper Llanvirn of the Builth area and showed that the number of pleural ribs varied in each lineage stratigraphically. In the case of *Whittardolithus* the number of ribs varied between 5.5 and 6.5 (see Systematics Chapter, *Whittardolithus*) but it is not known whether such fluctuations were a common feature of the Marrolithinae.

2.2 The Cephalic features of the Marrolithinae.

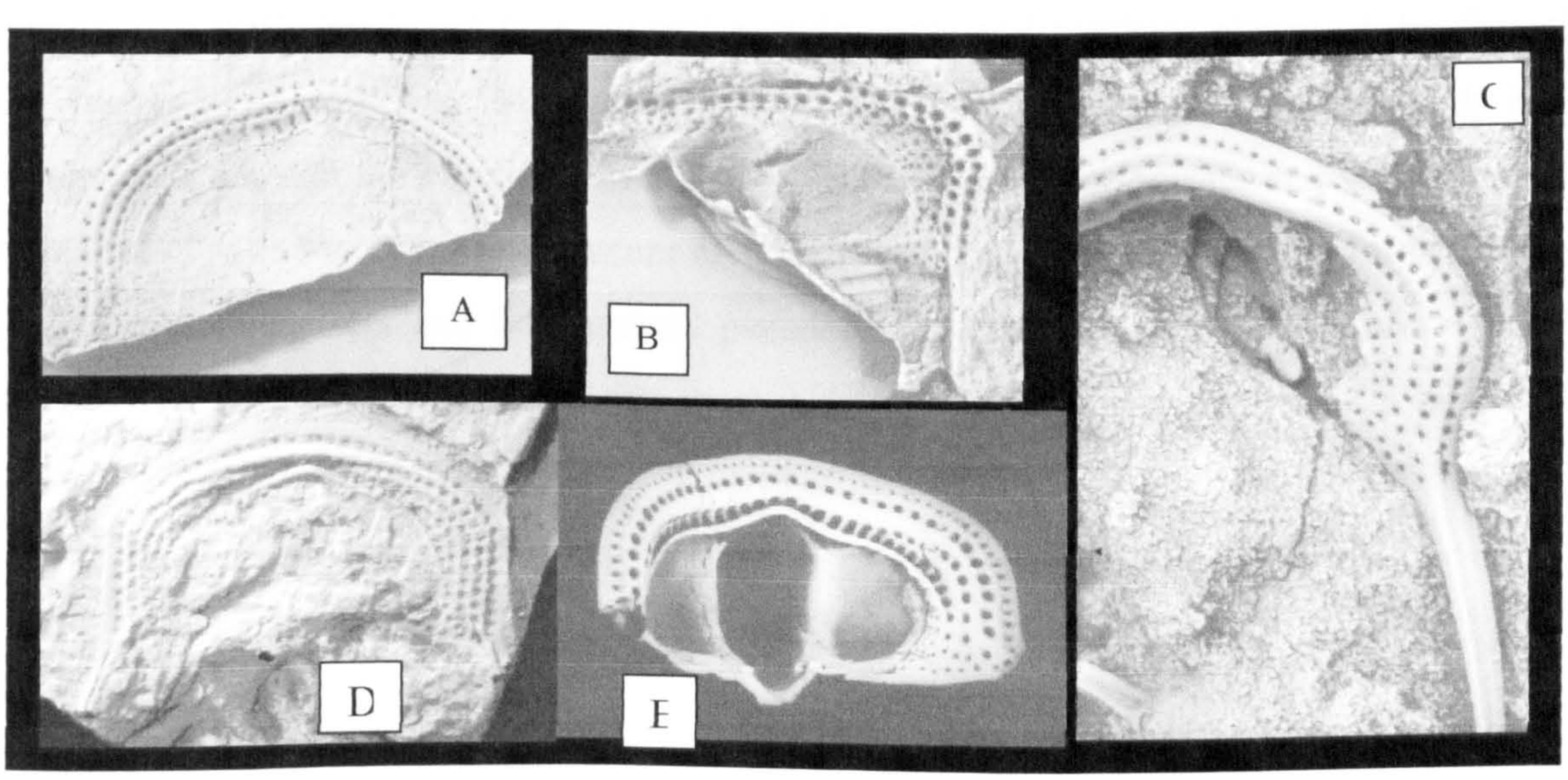
The Subfamily Marrolithinae is characterised (Hughes *et al.* 1975) by the well developed E, I and F pits, the termination of the inner most arc, I_n by the adjacent I arc, and generally some pit enlargement which invariably includes I_1. Extreme pit enlargement is commonly associated with fringe swellings on both the upper and lower lamellae. The glabella in all Marrolithinae is clavate and bears a median node. A short preglabellar field between the glabella and fringe area is present in species of *Protolloydolithus* and the genus *Lloydolithus*. 1p and 2p furrows are commonly distinct. The occipital pit and ring vary in definition between species as does the shape and even presence of an occipital spine. The genal lobes vary greatly in size and shape. Reticulation is generally seen in all meraspids. This strong surface sculpture covers the glabella and genal lobes, through ontogeny it is lost from the lower regions until only the topmost area of the glabella shows only fine reticulation. Juveniles also show tubercles extending from the glabella to mid way across the genal lobes. These may have had a sensory function. A feature preserved in crushed specimens is a strong ridge extending from around the 2p furrow outwards onto the genal lobe this may be homologous with the genal caecae seen in other trilobite families such as the Raphiophoridae, see Text-fig. 2.2.



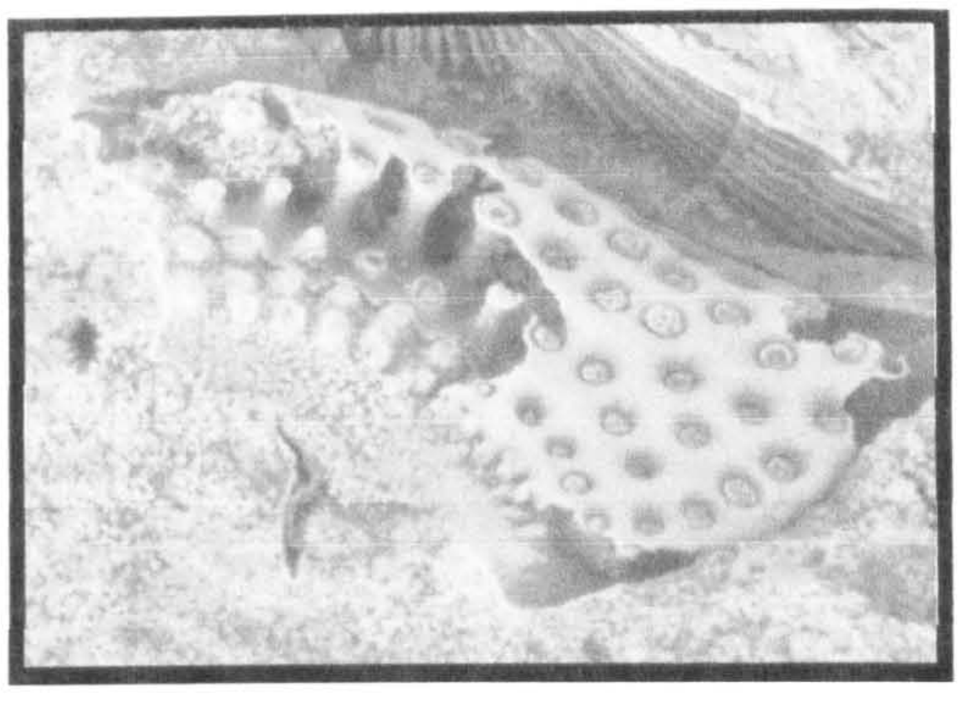
Text-fig. 2.2. A. *Whittardolithus superstes* x2 and B. *Lloydolithus lloydii* x2 specimens showing the ridge on the genal lobe which may be homologous to the genal caecae present in the Raphiophoridae.

2.2.1 Girder and pseudogirders.

The variable development of concentric ridges on the lower lamella is a generic level diagnostic feature within the Marrolithinae. The girder is recognised as the concentric ridge between arcs I_1 and E_1 which is confluent with the genal spine ridge and this latter feature can be used to assist in the identification of the girder (Text-fig. 2.3). Concentric ridges inward of the girder are known as internal pseudogirders and are numbered consecutively away from the girder. Correct identification of these features is paramount at generic level. *Deanaspis* and *Onnia*, show the genal spine ridge extending past the girder and joining up with the pseudogirders. Shaw (1995) used the bifurcation of the genal spine ridge as a diagnostic feature. He stated that in *Deanaspis* the ridge extends to both the girder and first internal pseudogirder and in *Onnia* the ridge passes straight to the first internal pseudogirder. Shaw (1995) believed that these ridge structures were important caecal channels. As can be seen in Text-fig. 2.3c and e, the genal ridge extension on to the fringe varies between the genera can therefore can not be used for classification purposes. Text-fig. 2.4 shows the relatively large gap between the lamellae and extra room provided by the ridge would be negligable.



Text-fig. 2.3. Lower lamellae showing various developments of the girder and first internal pseudogirder (A) distinct girder and first internal pseudogirder only developed weaky posterolaterally as seen here in *Whittardolithus superstes* x1, (B) distinct girder over fringe as in *Marrolithus craticulatus* x1, (C) equal development of girder and first interanl pseudogirder frontally as in *Deanaspis goldfussii goldfussii* x2, (D) distinct girder frontally with no pseudogirder development as in *Hammanaspis prima* x2 and (E) strong development of first internal pseudogirder with only a weak girder if present *Onnia ultima canthyle* x2.



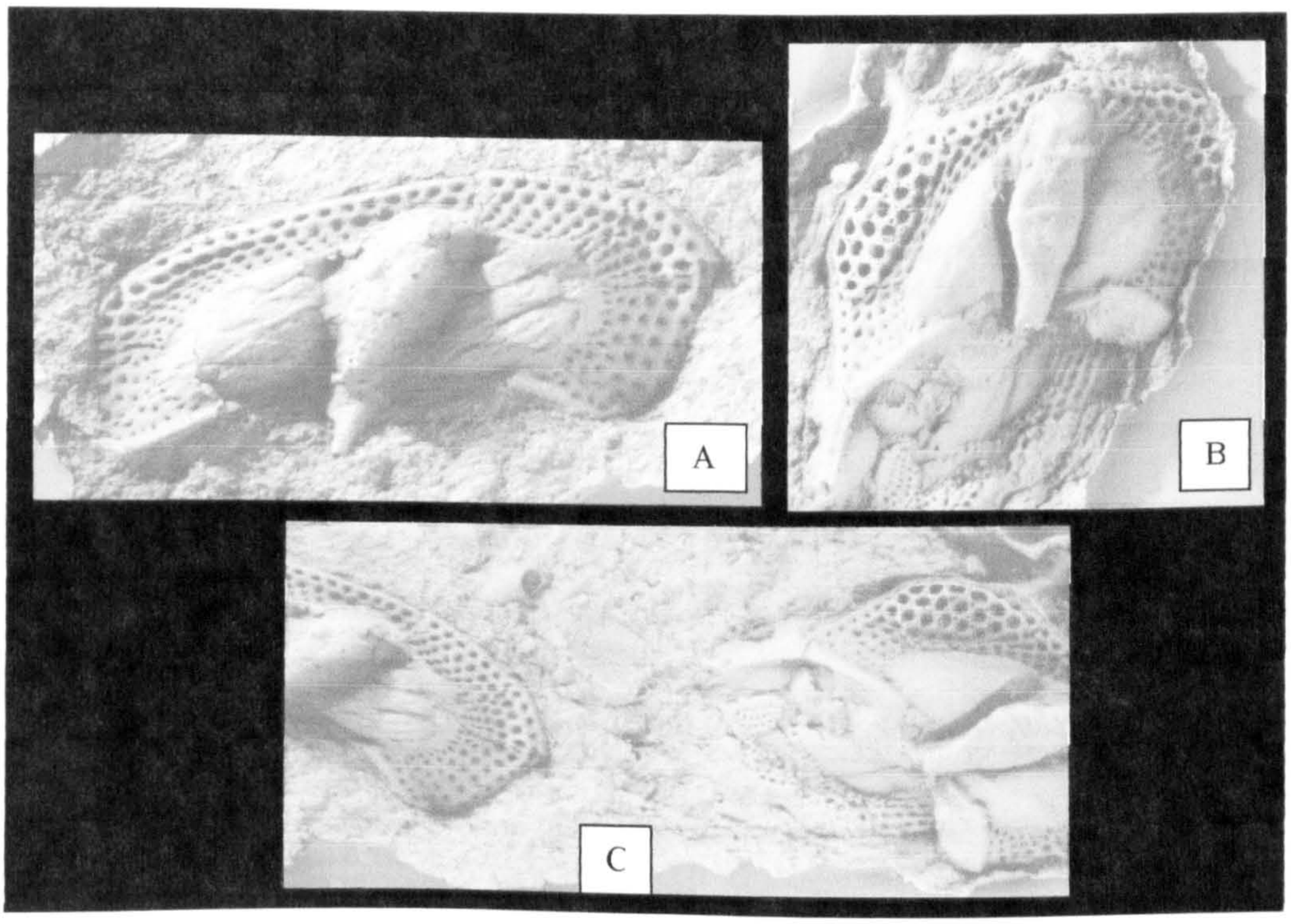
Text-fig. 2.4. Obique ventral view of *Onnia ultima canthyle* from Morocco (middle Caradoc) showing the funnel shaped pits and the gap between lamellae, x4.

There is a marked difference in the emphasis between the girder and first internal pseudogirder in *Onnia* and *Deanaspis* and these differences have been interpreted as a stratigraphical progression from the Llanvirn and Lower Caradoc *Marrolithus* with only a strong girder frontally through "transitional" mid Caradoc forms (*Deanaspis*) showing equally developed girder and first internal pseudogirder frontally to late Caradoc-early Ashgill forms (*Onnia*) with well developed first internal pseudogirder and weak or absent girder frontally (see Hughes *et al.* 1975, p.588; Shaw 1995, p. 13). During the course of this study it has become apparent that the condition of a strong first internal pseudogirder and weak or absent girder frontally, as seen in *Onnia,* occurs early and was contemporaneous with forms showing equally developed girder and first internal pseudogirder frontally, as in *Deanaspis*. Cladistic analyses (see Chapter 3) also shows that there is no linear relationship between *Deanaspis* and *Onnia* but that they likely have a common ancestor.

2.2.2 Genal lobe and fringe ratio.

There is a distinct relationship, within marrolithine genera, between the surface area of the fringe and that of the genal lobe. The most extreme cases are seen in *Marrolithoides* and *Protolloydolithus*. This relationship has long been recognised and has been used in the discrimination of *Marrolithoides* species. Using photographs of specimens of different

genera, the surface area of a genal lobe and a half fringe have been calculated for each specimen studied (Text-fig. 2.6). The results show that there is a marked difference between *Marrolithoides* and most other genera. *Protolloydolithus* shows similar marked differences. This approach can also be used on deformed specimens. Whittard (1956) had some doubt as to the identification of a specimen found alongside a *Marrolithus favus favus* individual and identified it as *Marrolithoides* cf. *anomalis* (see Text-fig. 2.5). The fringe to lobe ratio of this specimen in 1:0.81. *Marrolithus* show ratios around 1: 0.5 for undistorted material and *Marrolithoides* about 1:1.23 (see Text-fig. 4.9). It is likely therefore that Whittard's doubtful specimen is also *Marrolithus f. favus*.



Text-Fig. 2.5. Two individuals of *Marrolithus favus favus* showing different fringe inflation (A) is composed only of the cranidium [previously termed *Marrolithoides* cf. *anomalis* by Whittard (1956)], (B) is the complete cephalon and (C) shows the spatial relationship to each other.

Protolloydolithus neinstianus salax
(BGS 8528)
fringe to genal lobe ratio = 1 : 0.34

Lloydolithus lloydi
(BGS 86806)
fringe to genal lobe ratio = 1 : 0.60

Bettonolithus chamberlaini
(BGS 86786a)
fringe to genal lobe ratio = 1 : 0.74

Reuscholithus reuschi
(NHM In 42080 – holotype)
fringe to genal lobe ratio = 1 : 0.71

Whittardolithus superstes
[= *Whittardolithus inopinatus*]
(BGS 86792)
fringe to genal lobe ratio = 1 : 0.81

Whittardolithus superstes
[= *Whittardolithus instabilis*]
(NHM It 2793)
fringe to genal lobe ratio = 1 : 0.83

Marrolithus ultimus
[= *Costonia ultima*]
(NHM In 51708)
fringe to genal lobe ratio = 1 : 0.53

Marrolithus elegans
[= *Costonia elegans*]
(NHM It 10362)
fringe to genal lobe ratio = 1 : 0.82

A

Marrolithus favus favus
(SMCU A46910)
fringe to genal lobe ratio = 1 : 0.54

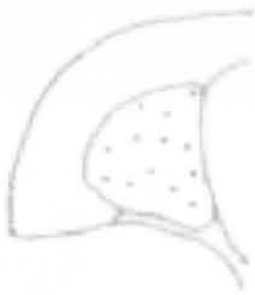
Marrolithus favus favus
(SMCU A46901)
fringe to genal lobe ratio = 1 : 0.50

Marrolithus favus favus
[= *Marrolithoides cf. anomalis*]
Wattison Collection W.23, fig'd by Dean 1956
fringe to genal lobe ratio = 1 : 0.81

Marrolithoides simplex
(NMW 83.31G.219)
fringe to genal lobe ratio = 1 : 1.23

Hammastaspis ornata
(MCZ 2218)
fringe to genal lobe ratio = 1 : 0.35

Hammastaspis orthogonia
(NHM It. 1200 - holotype)
fringe to genal lobe ratio = 1 : 0.56



Ornia gracilis
(NHM In. 52014/1)
fringe to genal lobe ratio = 1 : 0.56

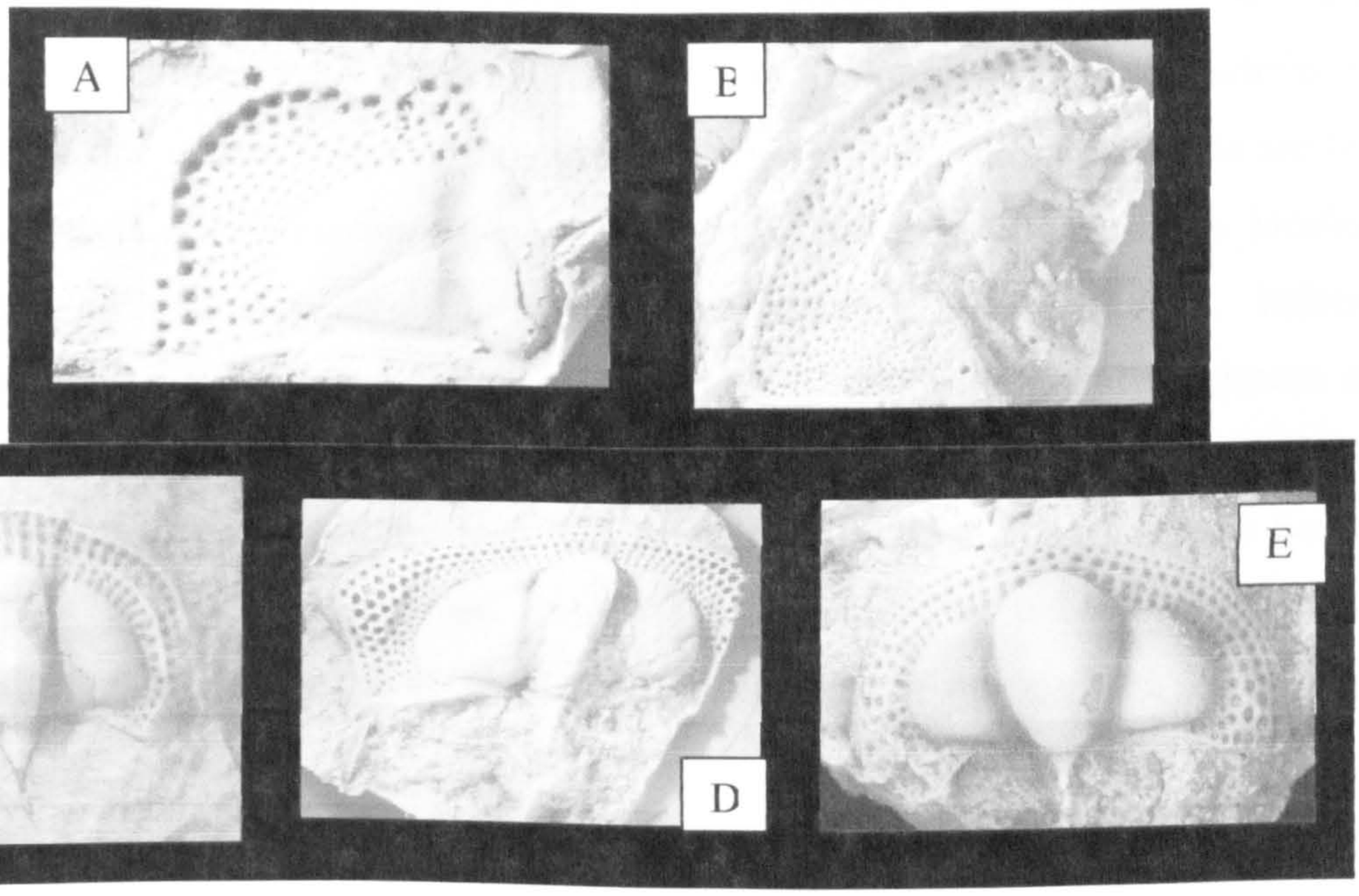
Decraspis goldfussii goldfussii
(UUG JV 1411
fringe to genal lobe ratio = 1 : 0.46

B

Text-fig. 2.6. A and B. Sketches showing halved cephala of species as recognised herein and their calculated fringe to genal lobe ratios. All drawings have been taken from photographs. The sketches are not to scale.

2.2.3 Fringe pit distributions and sizes.

The Marrolithinae contains perhaps the most diverse range of fringe pit patterns and pit sizes of any trinucleid subfamily. There is a general trend toward greater pit organisation through time. Thus the earliest genus *Protolloydolithus*, has only pits in arcs E_1, I_1, and I_n organised into arcs whilst the majority of the fringe is covered in randomly distributed pits. *Lloydolithus* and *Whittardolithus* show greater pit organisation but still retain an area of random pits posteriorly. *Bettonolithus*, *Marrolithus* and *Marrolithoides* exhibit varying high degrees of pit organisation. The progression culminates with the highly organised pit patterns of *Deanaspis* and *Onnia*. This stratigraphical trend has, however, two exceptions. *Marrolithus* (sensu lato) *elegans* [= formeraly *Costonia elegans*] and *Reuscholithus* contain areas of fringe with irregular pit patterns.



Text-Fig. 2.7. The overall stratigraphical increase in ordering of pit distribution illustrated by (A) *Protolloydolithus neintianus salax* (Llanvirn) x3, (B) *Lloydolithus lloydi* (Llanvirn) x2, (C) *Bettonolithus chamberlaini* (Llanvirn) x2, (D) *Marrolithus f. favus* (lower Caradoc) x2 and (E) *Onnia ultima canthyle* (upper Caradoc) x1.

With the exception of *Protolloydolithus* and *Marrolithus craticulatus*, all marrolithines have smaller pits in E_1 than in other arcs. The relative size of pits in particular arcs is diagnostic at the species and subspecies level. In some rare individuals the pits in all arcs appear much smaller than other specimens of the same species. These are thought to reflect a diagenetic thickening of the exoskeleton thus reducing the size of the pits.

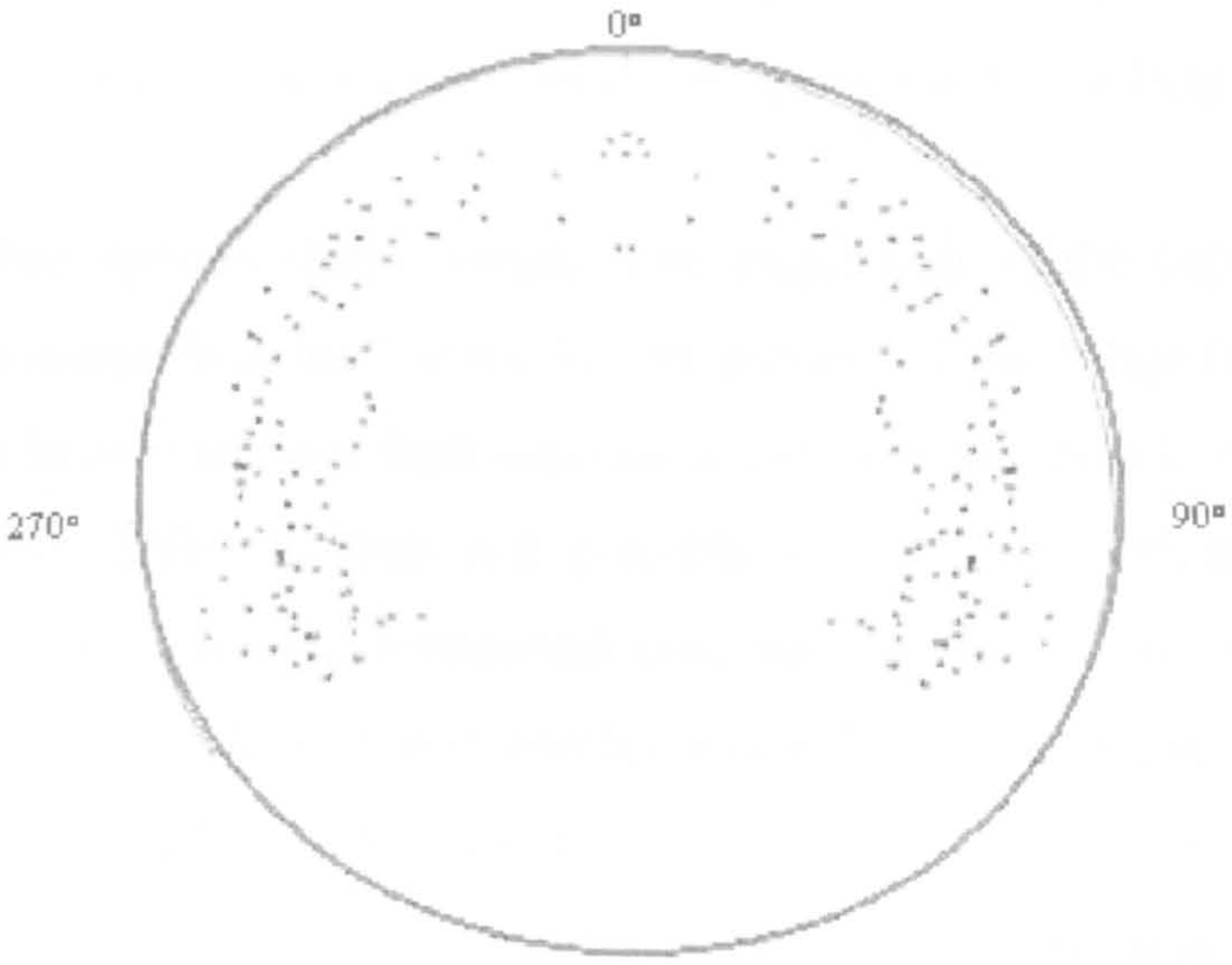
2.2.4 Fringe inflation.

The size, shape and elevation of pits on the upper, lower or on both lamellae are important diagnostic features at both generic and species level. Inflation is the elevation of the pit aperture relative to the general fringe surface. The majority of species within the Marrolithinae show one of two forms of inflation; one shows pit elevation in a single arc (e.g. in *Marrolithoides* and *Hammannaspis* gen. nov.), whilst the other form shows localised inflation of one or both lamellae involving a number of arcs (e.g. in *Marrolithus*). Inflation may or may not affect pit diameter. Fringe inflation is only seen in holaspid specimens and not in meraspid individuals. Lack of understanding of the temporal and spatial variation of fringe inflation within species has previously led to an over-divisive taxonomy (see Section 3.3). The degree of inflation observed can also vary depending upon the amount of taphonomic flattening, the direction of tectonic distortion and if one or both lamellae are present (see Text-Fig. 2.5).

2.2.5 Fringe Pit Function

There is a general consensus that the pitted fringe of trinucleids provided some kind of sensory function, although other uses have been suggested (Fortey and Owens 1999). An experiment to test the sensory field area was undertaken, using the same approach used by Clarkson (1966) and McCormick and Fortey (1998) to determine the visual field in trilobites. An undeformed cephalon of *Onnia u. canthyle* from Morocco was mounted on a

mineralogical universal stage, that could rotate around three axes. The cephalon was placed so that the sagittal line coincided with zero degrees on the horizontal rotation axis and the cephalon was tilted dorso-ventrally until its orientation matched that of specimens with genal spines horizontal to the substrate (see Hughes *et al.* 1975, p. 547). The poles to the pits on the upper lamella were calculated and plotted onto a stereogram (see Text-Fig. 2.8). The distribution of these points suggest that the field of presumed sensory pick-up was about five degrees to approximately 40 to 45 degrees from the horizontal. Although the points appear to be well distributed frontally and to the sides there was a slight increase in packing towards the posterior of the cephalon. A further test was carried out on a partial *Marrolithus favus* specimen and, significantly, the inflation of the pits typical for that species did not appear to affect the direction of the poles. The upper lamella could well have been used to collect information (light, vibration or chemical change) in the same plane as the trilobite. The lower lamellar pits proved more problematical to measure.

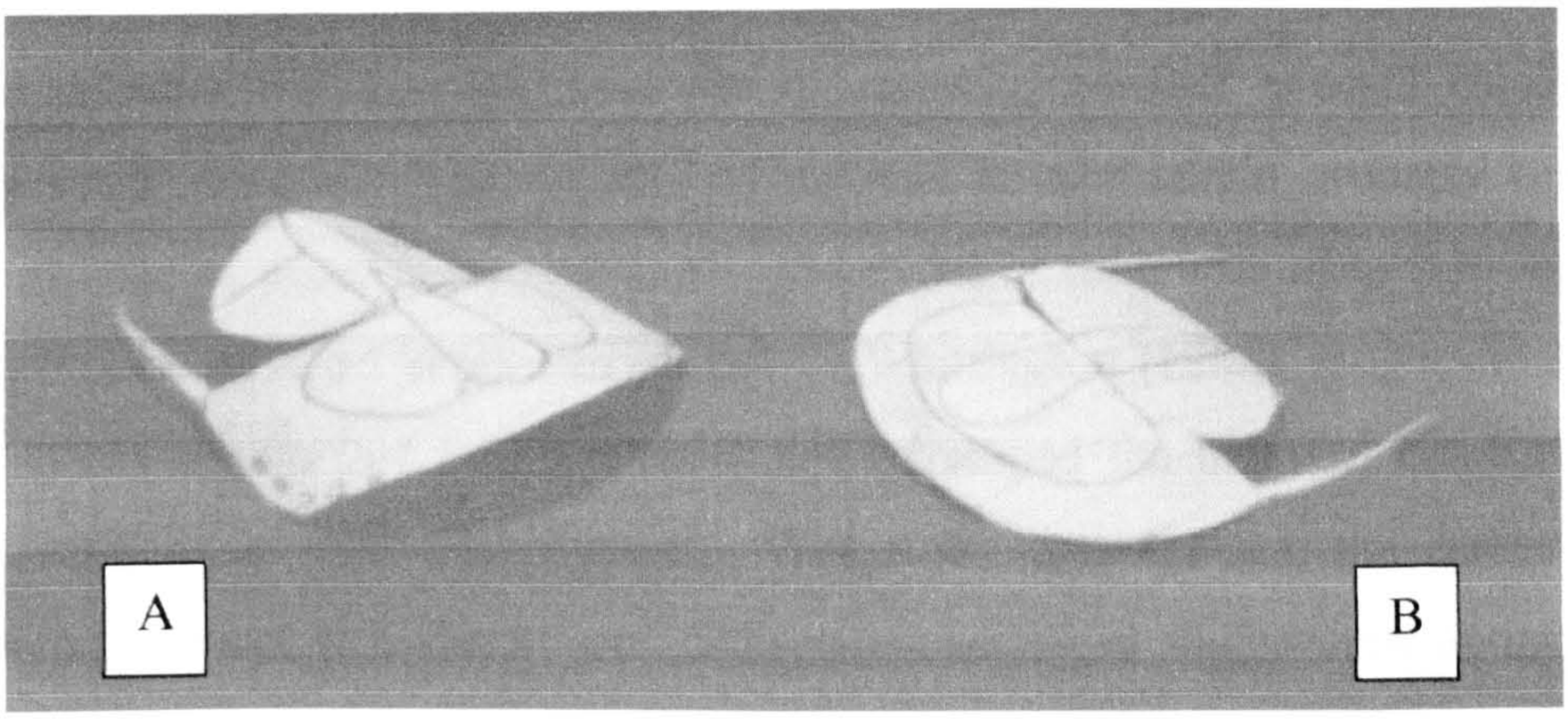


Text-Fig. 2.8. A upper hemisphere stereonet projection showing the poles to the pits of the upper lamella of an uncrushed *Onnia ultima canthyle*.

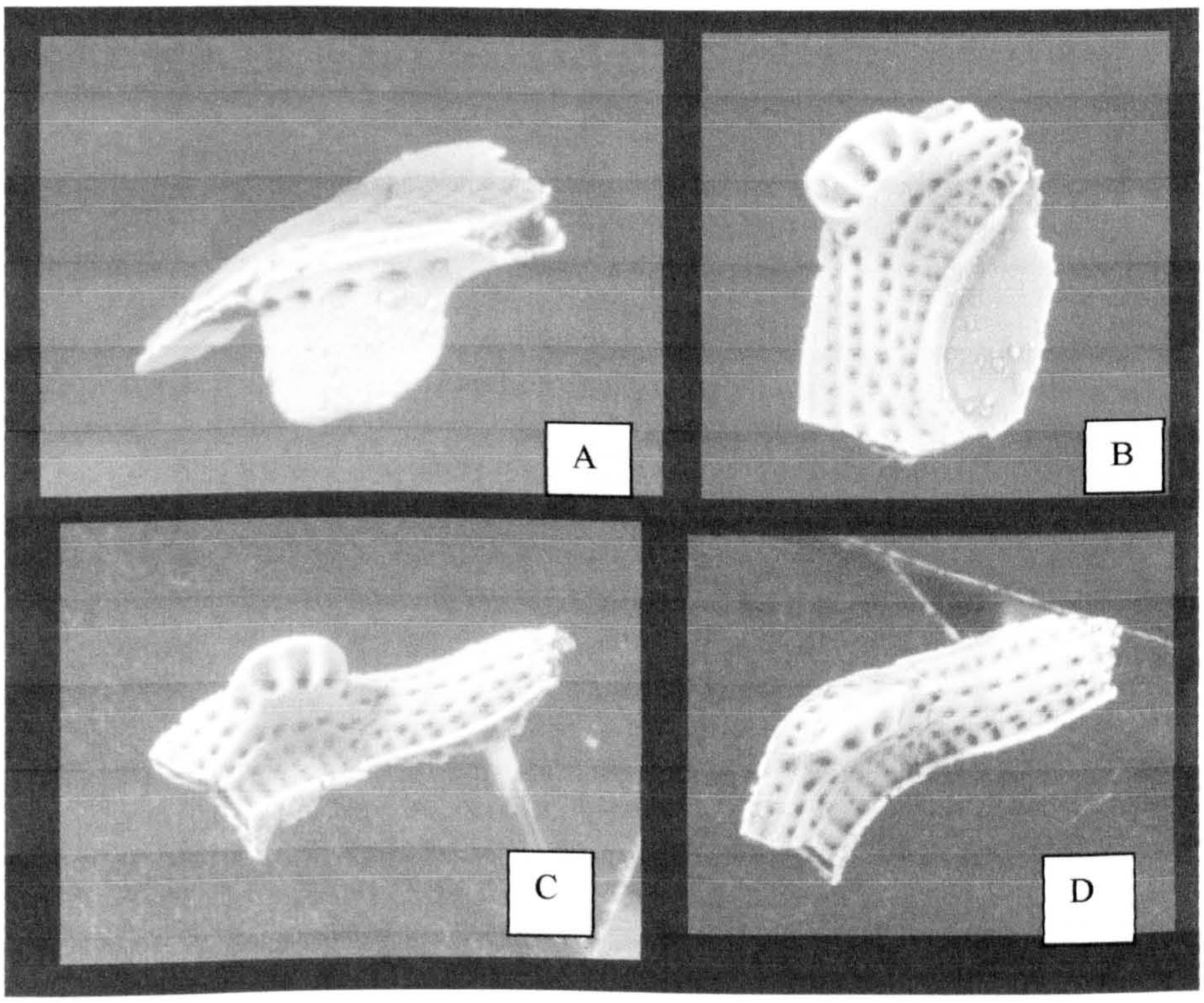
2.2.6 Cranidium outline

The outline of the cranidium can be diagnostic of different marrolithine genera and species. The shape is determined by the number and distribution of pits, fringe inflation, pit diameter, the presence or absence of an anterior arch and the curvature of the fringe. There may be a connection between cephalic outline and the local substrate. Card models of the different cephalic shapes were constructed. Simple semicircular models, representing *Protolloydolithus ramsayi*, *Lloydolithus*, *Bettonolithus* and *Whittardolithus*, show the cephalic margin including the genal spines would have evenly distributed the weight of the cephalon on the substrate (see Text-Fig. 2.9), similar to present day *Limulus*. The cephalon would have been a substantial proportion of the weight of the living trilobite, containing the main organs as well as the majority of the mineralised test. The semicircular outline could therefore allow the individual to rest on soft sediments without sinking. Due to diagenetic flattening it is unclear whether *Protolloydolithus neintianus* and *P. n. salax* possessed an anterior arch. Models of these species show a similar case to the semicircular cephala if the fringe was indeed flat. However, if an anterior arch was present the amount of forward tilting, and therefore instability, that occurred was directly proportional to the height of the arch.

Certain *Marrolithus* species show considerable angulation of the cephalic outline and some individuals also possess "notches" at the lateral corners of the fringe (see Pl.1. Figs 7 and 8). These species are known to have high anterior arches and the models showed them to be very stable(see Text-Fig. 2.9). It was not possible to tilt them forwards. Younger genera (*Deanaspis* and *Onnia*) have sub-rounded outlines but they show a great variation in the anterior arch height. The low arched species would have been more stable in water flowing from behind than the higher arched species and may reflect the preferred water dynamics of the different species. Inflation would not have affected these findings as the curvature of the fringe was sufficient to keep the inflations and girder/pseudogirder developments on the lower lamella out of contact with the substrate. However, some *Marrolithus* (s. l.) *elegans* specimens from Avalonia that show deep "keel" like structures on the lower lamella (Text-Fig. 2.10) which may have acted as stilts or may have been sunk into the substrate as anchors or for sensory use.



Text-Fig. 2.9. Two card models representing (A) *Marrolithus favus favus* showing quadrate fringe and (B) *Whittardolithus superstes* displaying a subrounded cephalic outline. Note the differing amounts of cranidium in contact with the substrate. Type A was more stable than card models with less distinct lateral extentions.



Text-Fig. 2.10. Two silicified Welsh specimens of *Marrolithus* (s. l.) *elegans* showing extended girder producing a ventral "keel" anterolaterally. (A) and (B) BNHM It10342 and (C) and (D) BNHM It10343 all x7.

2.2.7 Ontogeny.

Complete exoskeletons are necessary in order to ascertain whether a small trilobite is a meraspid or a small holaspid. The majority of material studied herein probably represents disarticulated exuviae or possibly posthumously scavenged or otherwise disturbed debris and so is of little ontogenetic use. Work carried out by Whittington (1968), Hughes (1971) and Addison (1974) has shown that juvenile trinucleids developed the holaspid number of arcs and pits very early on in their development. Within the marrolithines, the earliest arc to develop, in meraspid stage 1, is the In arc. Subsequent meraspid stages show an increase in ordering of the pits and development of the other I and E arcs (for example Pl. 7, Fig. 4 shows a possible meraspid stage 2), until by stage 5, the final, stable pit distribution was reached (see Pl. 10, fig. 1 showing meraspid stage four and five marrolithines.

3 CLADISTIC ANALYSIS

3.1 Diagnostic characters and phylogenetic relationships determined by Hughes et al. (1975)

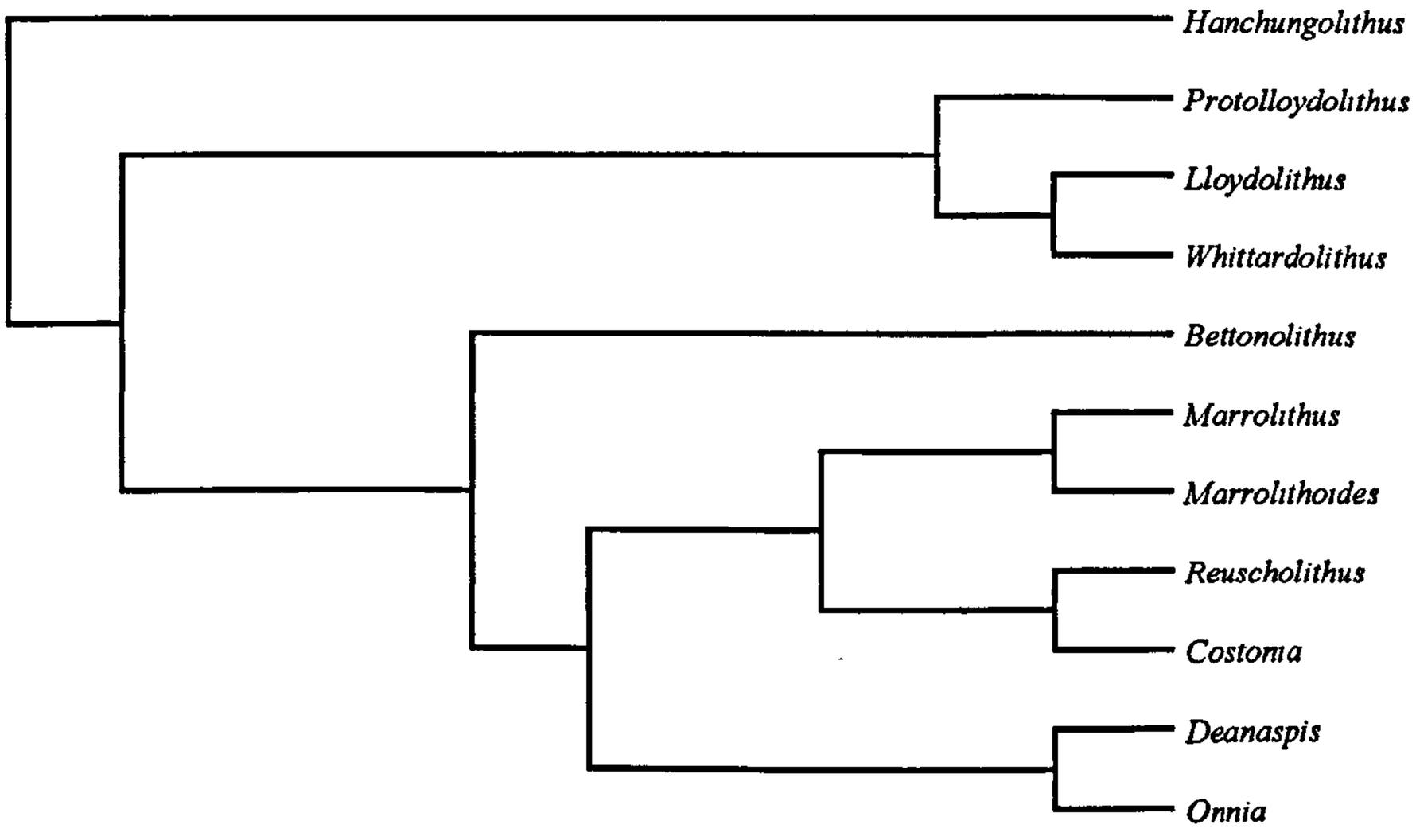
Hughes *et al.* (1975, pp. 582-588, fig. 120) proposed a phylogeny based on the qualitative assessment of the Marrolithinae as part of their wider analysis of the Trinucleidae (see Fig. 3.1). Cladistics were used in the present study to test this phylogeny using the cephalic characters which Hughes *et al.* considered to be diagnostic of each genus. However, not all characters were used in every diagnosis given by Hughes *et al.* and in those cases a new assessment of the type species has been used herein to provide the missing data. The characters and their states together with their codings are as follows:

- fringe shape [outline of the cephalon]: 0-sub-quadrate, 1-sub-semicircular, 2-varied [a range of outlines], 3-semicircular.
- pit inflations [pits raised above the surface of the fringe]: 0-absent, 1-present.
- girder: 0-well developed, 1-weak.
- first internal pseudogirder: 0-absent, 1-present, 2-prominent.
- girder list [thin ridge on upper lamella above position of girder]: 0-poor, 1-sharp.
- glabellar height to apex of glabella from axial furrows: 0-low, 1-medium, 2-high.
- radial sulci: 0-absent, 1-present.
- outermost arc: 0-I_1, 1-E_1, 2-E_2.
- Arc E_2: 0-absent, 1-only present anteriorly, 2-extensive.
- large pits:0-absent, 1-$I_1 + I_2$, 2-$I_1 + E_1$, 3-$I_n + I_1$.
- irregularly distributed pits: 0-present, 1-absent.

- preglabellar field [narrow pitless area in front of the glabella]: 0-present, 1-absent

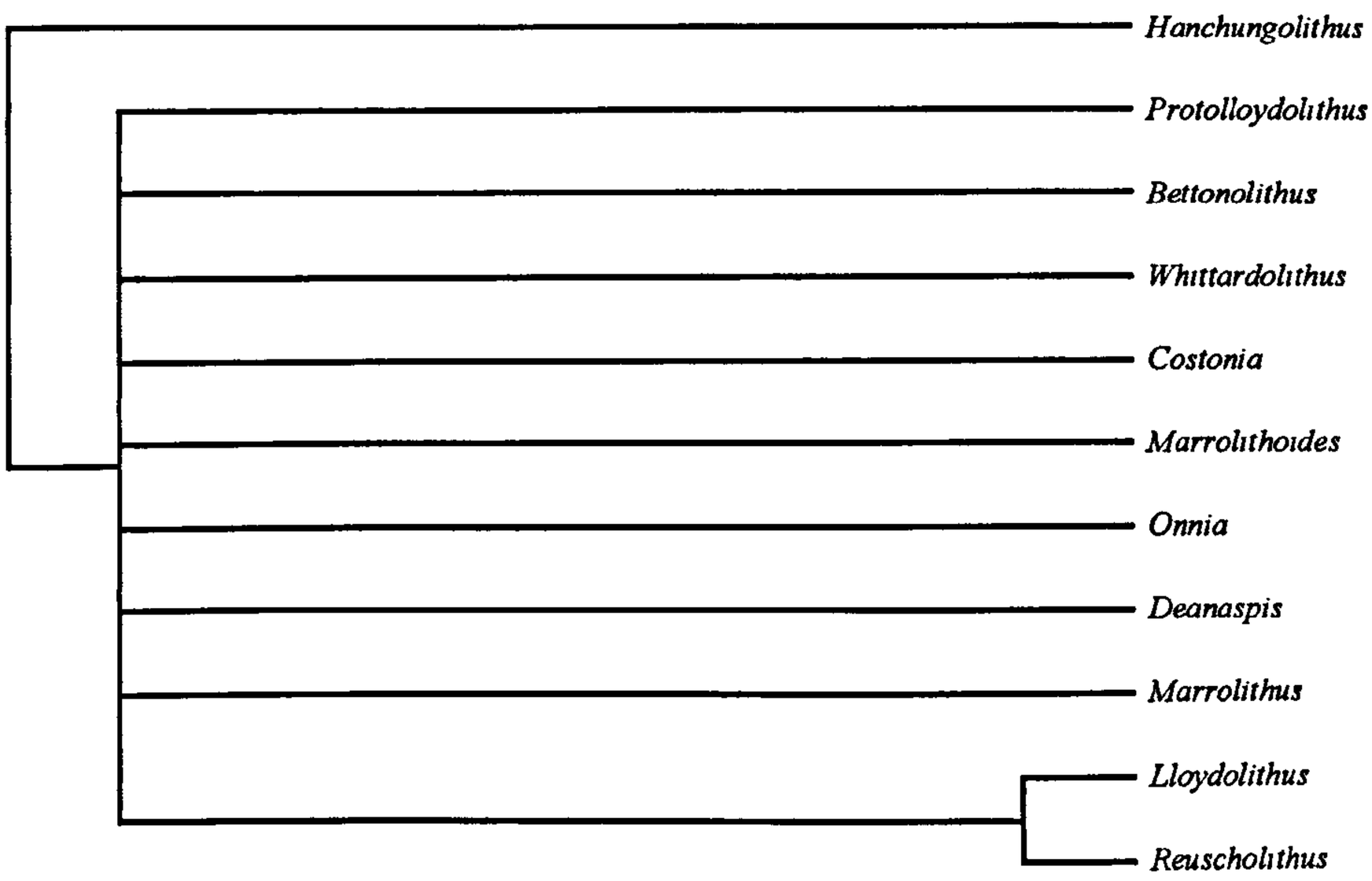
Some of the characters states (e. g. outermost arc, presence of E_2 and irregular pits) are easier to code or define unequivocally than others (e. g. glabellar height, fringe inflation, girder list, pseudogirder). These more subjective characters were omitted from many of the generic diagnoses by Hughes *et al.* (1975) and needed to be provided for this analysis. The genus *Hanchungolithus* Lu, 1954 is the most likely ancestral group for the Marrolithinae (Hughes *et al.* 1975; Fortey and Owens 1987) and type species *Hanchungolithus primitivus* (Born, 1921) was used as the outgroup for the cladistic analysis. Table 1 shows the information used, italics refer to information not given in the diagnoses by Hughes *et al.*, but coded from the type species concerned. For more detailed information on cladistic analyses see Swofford (1990) and Wiley *et al.* (1991).

Using the programme MacClade version 3.0, the topology of the phylogeny as described by Hughes *et al.*, (1975), produced a tree of length 38 and a consistency index (CI) = 0.53 (Text-Fig. 3.1). The consistency index reflects the "fit" of the data and the transformation series to a particular tree. A tree with a high value (near 1.0) shows little or no homoplasy (i. e. convergence, reversals or parallelisms); trees with low values show considerable homoplasy. Generally each diagnostic character shows some degree of homoplasy.



Text-Fig. 3.1. Phylogeny of the Marrolithinae as proposed by Hughes *et al.* (1975) expressed as a cladogram.

Analysis of the generic diagnosis characters of Hughes *et al.* (1975) using PAUP 3.0 produced 31 equally parsimonious trees (tree length 34, Rohlf's CI = 0.22). The strict concensus tree shows no subclades (Text-Fig. 3.2). This suggests that the present diagnostic features are a mixture of autapomorphies and characters that are: (i) ill-constrained or, (ii) difficult to quantify, e.g., glabellar height: "short", "medium", "high", or (iii) show a high degree of homoplasy. The published classification of the Marrolithinae therefore does not lend itself to cladistic analysis and if such analysis is to help clarify the phylogeny of the subfamily, the characters and character states must be more tightly constrained and new characters sought.



Text-Fig. 3.2. The consensus tree generated by PAUP using the generic diagnostic characters of Hughes *et al.* (1975).

3.2 Characters used in this study

Characters were coded using the holotype or lectotype of each species that is currently recognised. In cases where this type specimen was not well enough preserved to show a character, the paratypes or syntypes or failing them, topotypes were used. This approach was used to eliminate gaps in the data as PAUP attempts to apply all possible states of a character that is coded as missing data and this may lead to a large number of trees being generated to accomodate the uncertainty in the data set. Also, if a number of taxa show missing data these could be grouped together due to mutual lack of information. The characters chosen are discrete (presence/absence) features, features based on clearly defined states or those divided arbitrarily. Characters codified by the last method were used primarily to describe fringe inflation features which in themselves show some degree of variation. Overall, it is difficult to find discrete characters that do not show variation within a

species. Some features used previously to define genera or species do not lend themselves to cladistic analysis (such as glabellar shape and size, degree of anterior arch development) are listed at the end of this section. Their omission from the cladistic analysis does not completely reduce their usefulness in more qualitative classification.

Ideally, generic diagnostic characters should show up in the analyses as synapomorphic features of subclades of species within the Marrolithinae. However, it is not possible to show the variation within populations using type species alone and therefore these variations in characteristics must be taken into account when interpreting the phylogeny suggested by the cladistic analysis. Cladistic results at the species level are described in detail for each genus in the appropriate section of the systematics chapter (Chapter 4).

Note that the names applied to the specimens used to illustrate character states in this chapter are those resulting from the taxonomic revision undertaken in the present study. The cladistic analysis, however, was undertaken on the taxa as hitherto understood.

3.2.1 Characters used for species analysis

1. Outline of the cephalon (Text-Fig. 3.3)

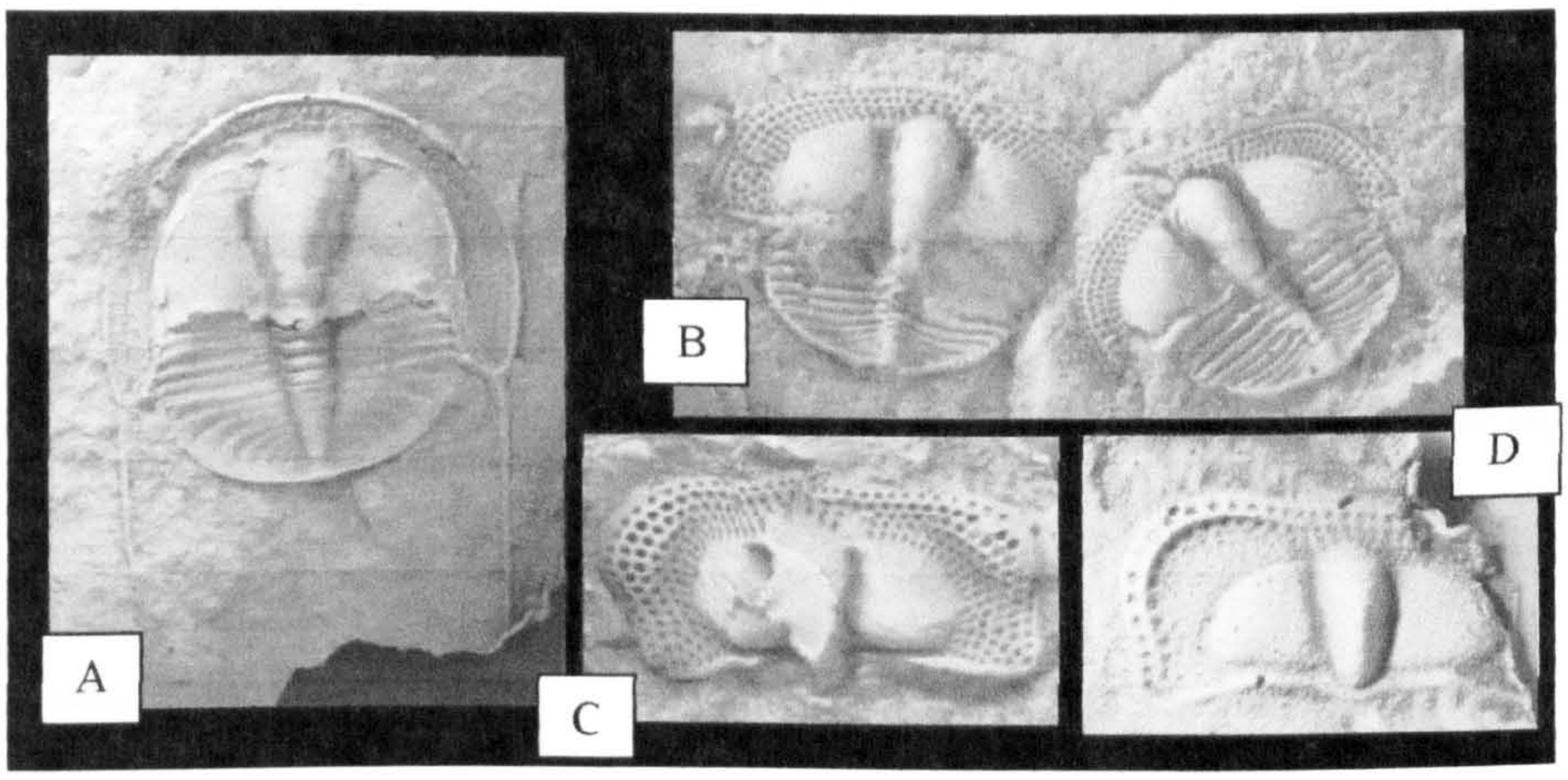
This can be a highly variable character but generally there are four easily defined states:

0 - rounded

1 - subquadrate, mesial edge in front of lateral corners in dorsal view.

2 - subquadrate, mesial edge at the same level as lateral corners in dorsal view.

3 - subquadrate, mesial edge behind lateral corners in dorsal view.



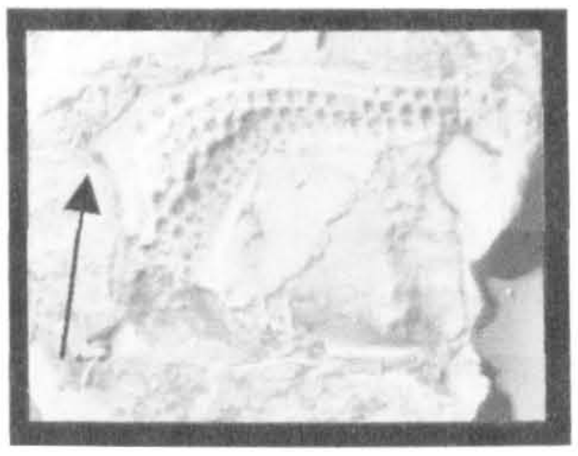
Text-Fig. 3.3. Character states in the outline of the cephalon. A. rounded (*Lloydolithus lloydi*) x2.5. B. subquadrate, mesial edge in front of lateral corners in dorsal view (*Deanaspis goldfussii*) x4. C. subquadrate, mesial edge at the same level as lateral corners in dorsal view (*Marrolithus favus*) x2. D. subquadrate, mesial edge behind lateral corners in dorsal view (*Protolloydolithus salax*) x2.5.

2. Lateral margin extension (Text-Fig. 3.4)

The antero-lateral margin of the fringe may be slightly expanded (transversely) such that its edge curves away from, rather than lying parallel to, E_1.

0 - absent

1 - lateral extension present



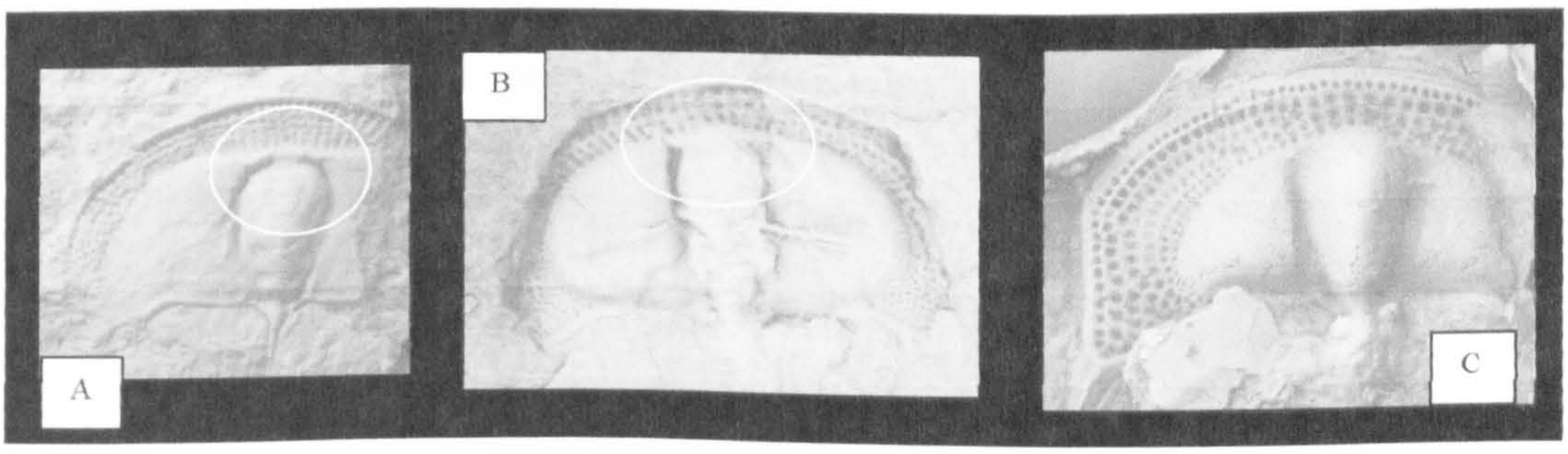
Text-Fig. 5.4. *Marrolithus favus* showing lateral extension, x5.

3. Preglabellar field (Text-Fig. 3.5)

This is a narrow area of the fringe that lies between the inner arc and the front of the glabella:

0 - absent

1 - present



Text-Fig. 3.5. Two examples of preglabellar field. A. *Lloydolithus lloydi* x2 and B. *Whittardolithus superstes* x3 and C. *Deanaspis goldfussii goldfussii* x3, showing an example of no preglabellar field.

4. Genal lobe : fringe area (Text-Fig. 3.6)

The area of half-fringe compared to that of one genal lobe, calculated using a photograph of a dorsal view of a flattened but otherwise undistorted specimen (see Section 2.2.2 for details).

0 - fringe : lobe (1 : < 0.40)

1 - fringe : lobe (1 : 0.41 - 0.59)

2 - fringe : lobe (1 : > 0.60)

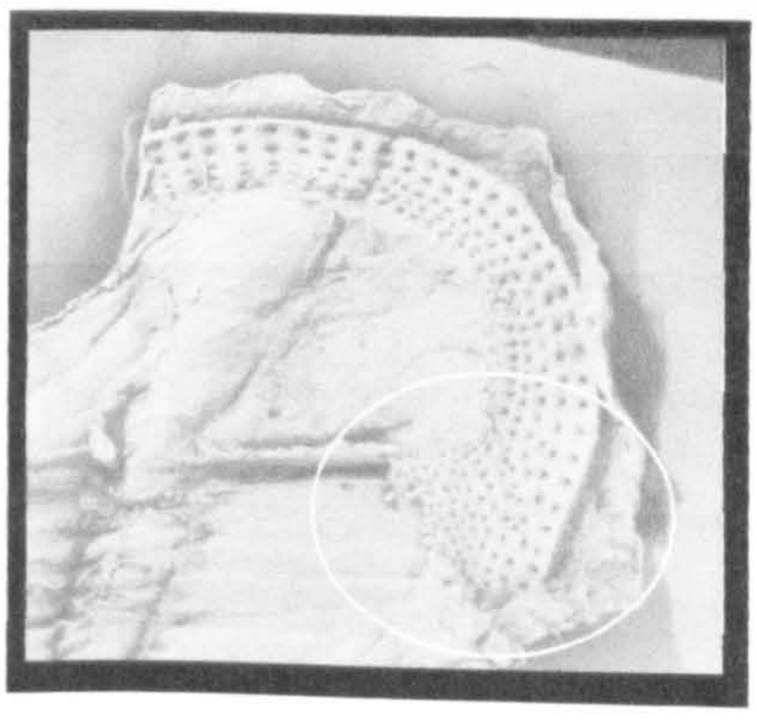
3 - fringe : lobe (<1 : 1)

5. Genal prolongation (Text-Fig. 3.7)

The genal area extends beyond the level of the occipital ring. Some species showing only a slight posterior extension of genal area are coded in the same way as those lacking a prolongation:

0 - prolongation absent

1 - significant prolongation present



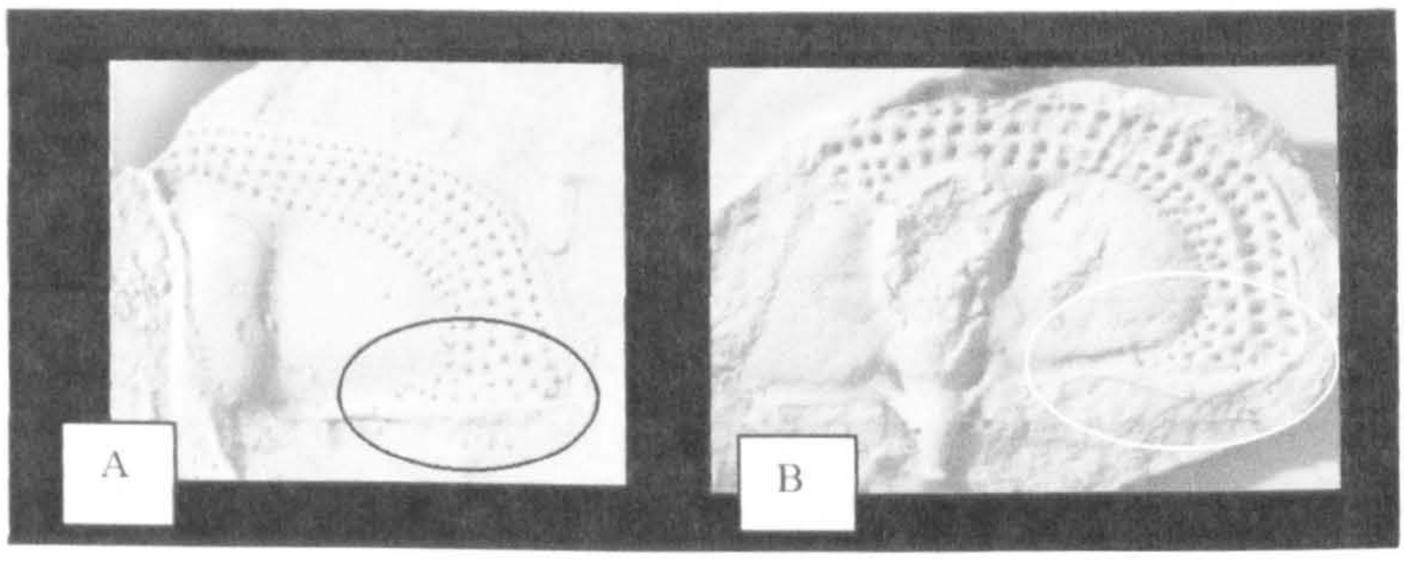
Text-Fig. 3.7. *Whittardolithus superstes* showing genal prolongation x3.

6. Posterior margin extension (Text-Fig. 3.8)

Margin between genal angle of cranidium and occipital furrow protrudes rearwards further than genal angle.

0 – margin extension absent

1 – extension present



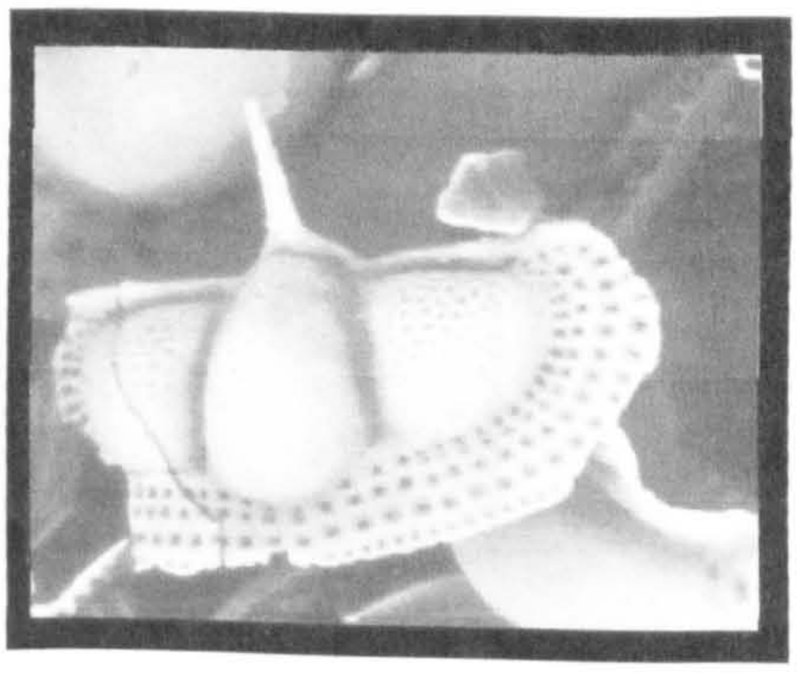
Text-Fig. 3.8. A. margin extension absent (*Deanaspis goldfussii*) x4. B. margin extension present (*Bettonolithus chamberlaini*) x4.

7. Occipital spine (Text-Fig. 3.9)

The absence of a spine is only characteristic at species level, with the exception of the genus *Protolloydolithus* where it is absent in all described species.

0 - absent

1 - present



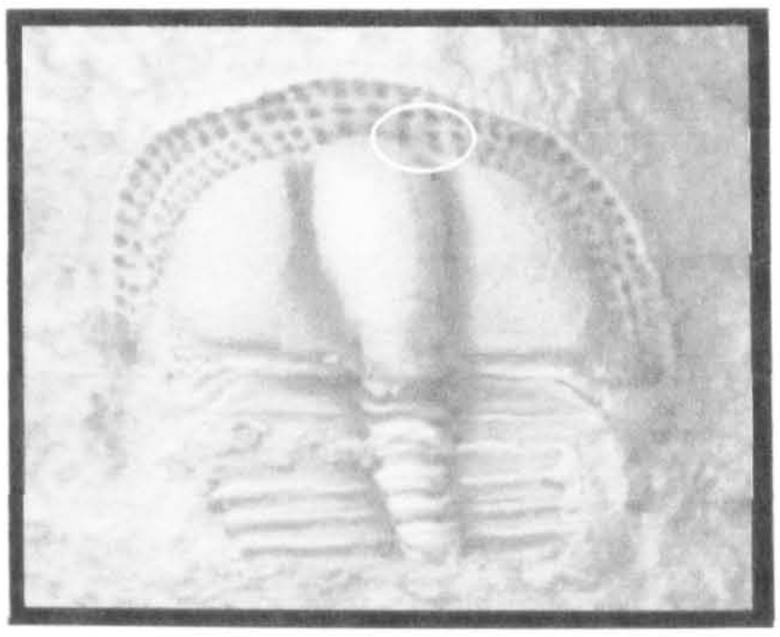
Text-Fig. 3. 9. Silicified *Onnia ultima ultima* showing occipital spine x7.

8. Sulcate pits (Text-Fig. 3.10)

Two or more pits in any adjacent arcs sharing a depression in the anterior fringe area.

0 - absent

1 - present



Text-Fig. 3.10. *Bettonolithus chamberlaini* showing sulcate I_n and I_2 pits, x4.

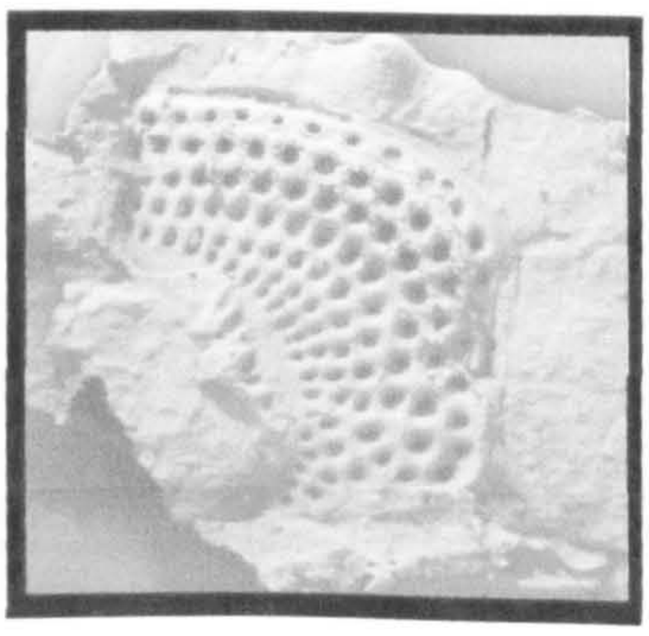
9. Radial alignment of pits (Text-Fig. 3.11)

Radial alignment of pits in the inner arcs (I_1 to I_n). The pits may, or may not, share sulci:

0 - absent

1 - present to lateral part of the fringe

2 - present to posterior area of fringe



Text-Fig. 3. 11. *Marrolithus favus favus* showing radial alignment of pits to near the posterior of the fringe, x2.

10. E_2 arc

The E_2 arc is a relatively rare feature within the Marrolithinae. The majority of genera show no E_2 arc development or it is only partially developed frontally. The genus *Lloydolithus* is the only one to show complete development of E_2.

0 - absent

1 – present frontally

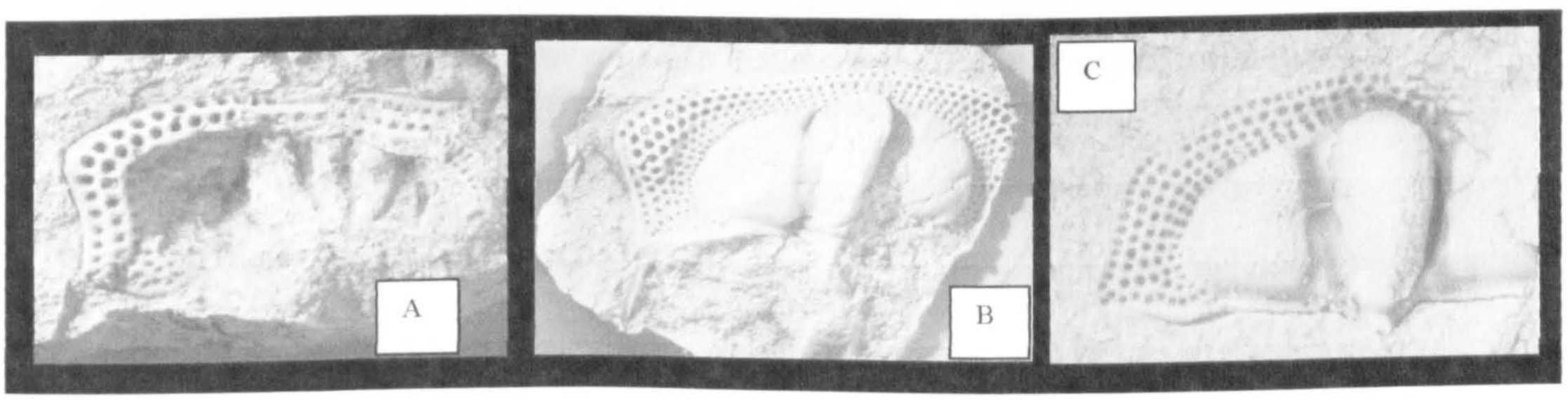
2 - continuous around fringe

11. E_1 arc pit packing (Text-Fig. 3.12)

Some species show considerable pit alignment between the E_1 and I_1 arcs as a consequence of having similar pit counts in these arcs. Others show E_1 pits misaligned and closer together than the I_1 pits:

0 –E_1 pit count ~ I_1 pit count – E_1 well spaced

1 - E_1 pit count > I_1 pit count – E_1 pits closely packed



Text-Fig. 3.12. A. well spaced E_1 pits, *Marrolithus craticulatus*, x4. B. *Marrolithus f. favus*, x3 and C. *Deanaspis primotina*, x4 showing E_1 pits closely packed.

12. E_1 arc pit diameter

0 - E_1 pits are larger than inner pits

1 - E_1 pits are of similar diameter or smaller than inner pits

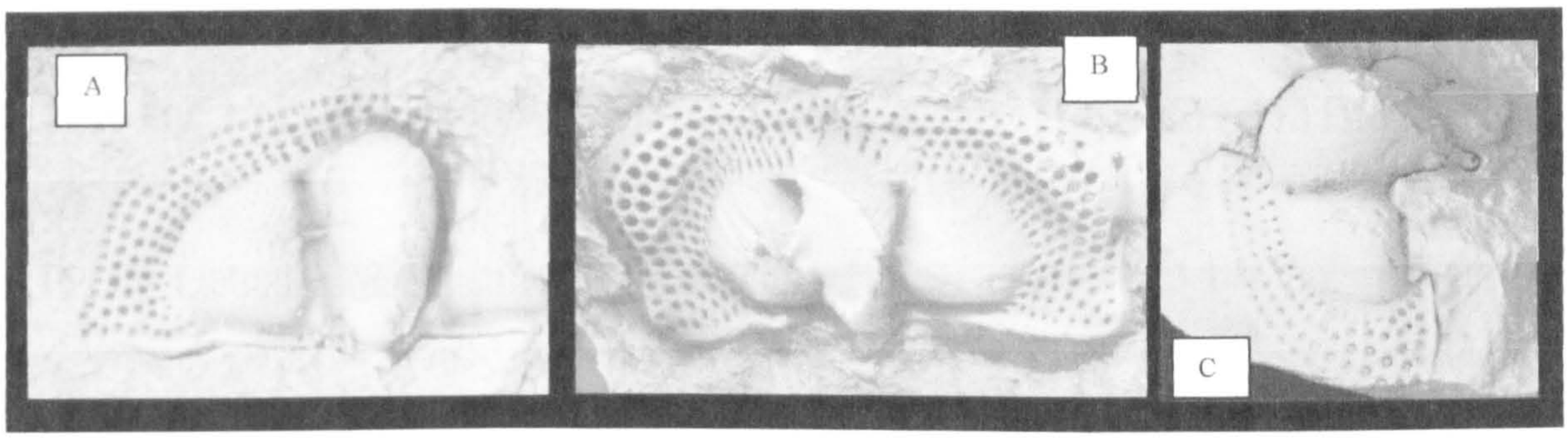
13. I_1 arc pit width (Text-Fig. 3.13)

0 - I_1 pit width is similar to majority of other pits

1 - I_1 pit width increases to a maximum at the lateral area of the fringe

2 - I_1 pit width increases to a maximum at the posterior area of the fringe

3 - I_1 pit width larger than other arcs along entire fringe



Text-Fig. 3.13. A. large I_1 pits over all fringe (*Deanaspis primotina*), x4. B. I_1 pit diameter increases to a maximum in the lateral position (*Marrolithus favus*), x3.5. C. I_1 pit diameter increase to a maximum near the posterior margin (*Onnia ultima ultima*), x3.

14. I_2 arc pit width

0 - I_2 pit width does not follow I_1 pit diameter changes

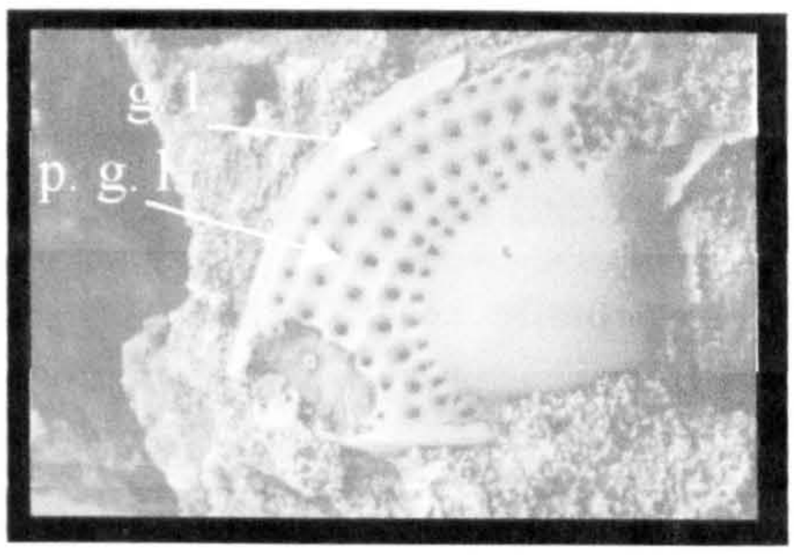
1 - I_2 pit width is similar I_1 pit diameter changes

15. Girder list on the upper lamella (Text-Fig. 3.14)

Concentric ridge between E_1 and I_1:

0 - absent or indistinct

1 - conspicuously broad or sharp



Text-Fig. 3.14. *Onnia ultima canthyle* showing distinct girder list (g. l.) and first internal pseudogirder list (p. g. l.), x3.

16. First internal pseudogirder list on the upper lamella (Text-Fig. 3.14)

0 - none

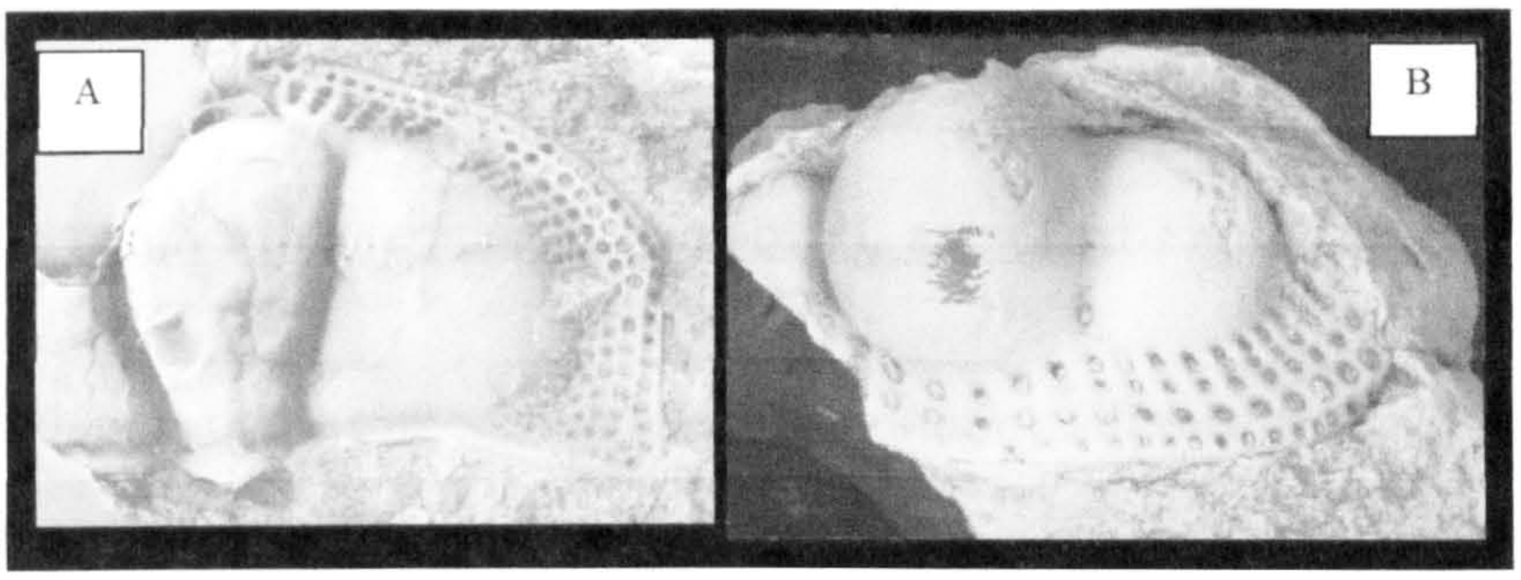
1 - first internal pseudogirder list conspicuous

17. Tilted E_1 arc (Text-Fig. 3.15)

The E_1 arc in the lateral-posterolateral area of fringe may be tilted downwards in uncrushed specimens, this is usually accompanied by a distinct list between E_1 and I_1.

0 – E_1 arc tilt absent

1 - E_1 arc tilt present



Text-Fig. 3.15. Two examples of E_1 tilting: A. *Marrolithoides simplex*, x4. B. *Onnia ultima cobboldi*, x5.

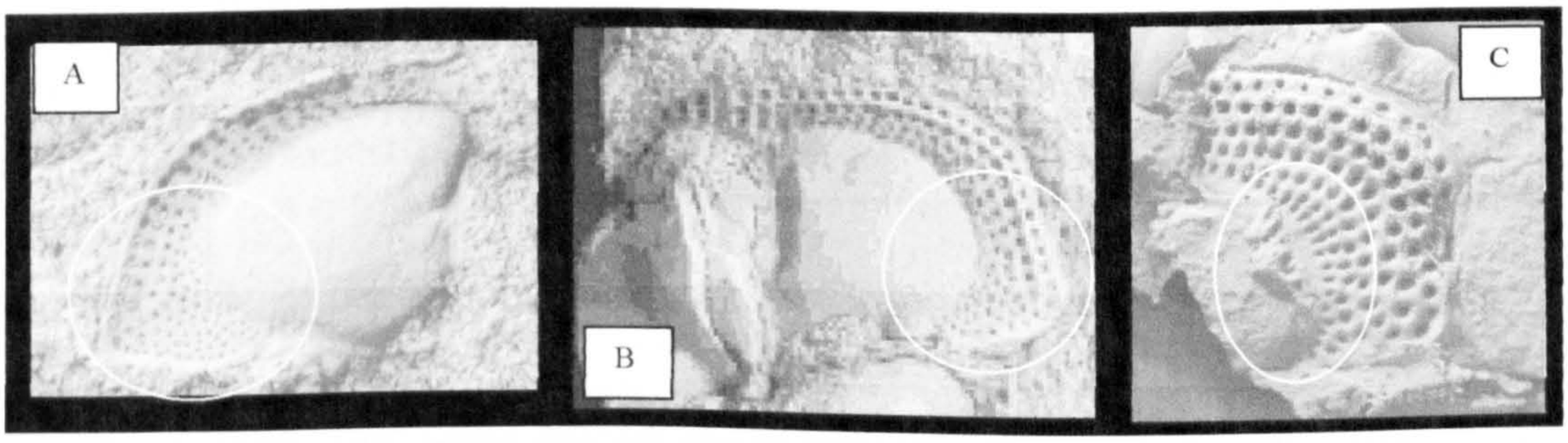
18. F and irregular posterior pits (Text-Fig. 3.16)

Flange pits (F pits) are pits developed on the face of the flange of the lower lamella. On the upper lamella they are seen as small pits at the inner edge of the fringe internal to arc In. Some species also show small irregular pits on the posterior of the fringe which are indistinguishable from the F pits when viewed on the upper lamella. The development of these pits falls into three generally quite distinct groups, listed below.

0 - extensive

1 – covering moderate area (about 20 pits)

2 - a few pits immediately adjacent to genal lobes (<15 pits)



Text-Fig. 3.16. A. extensive F pit development (*Whittardolithus superstes*), x3. B. moderate development (*Marrolithoides simplex*), x4. C. only a few F pits developed adjacent to genal lobes (*Marrolithus favus favus*), x2.

19. Arc number that terminates (cuts-off) I_n arc (Text-Fig. 3.17)

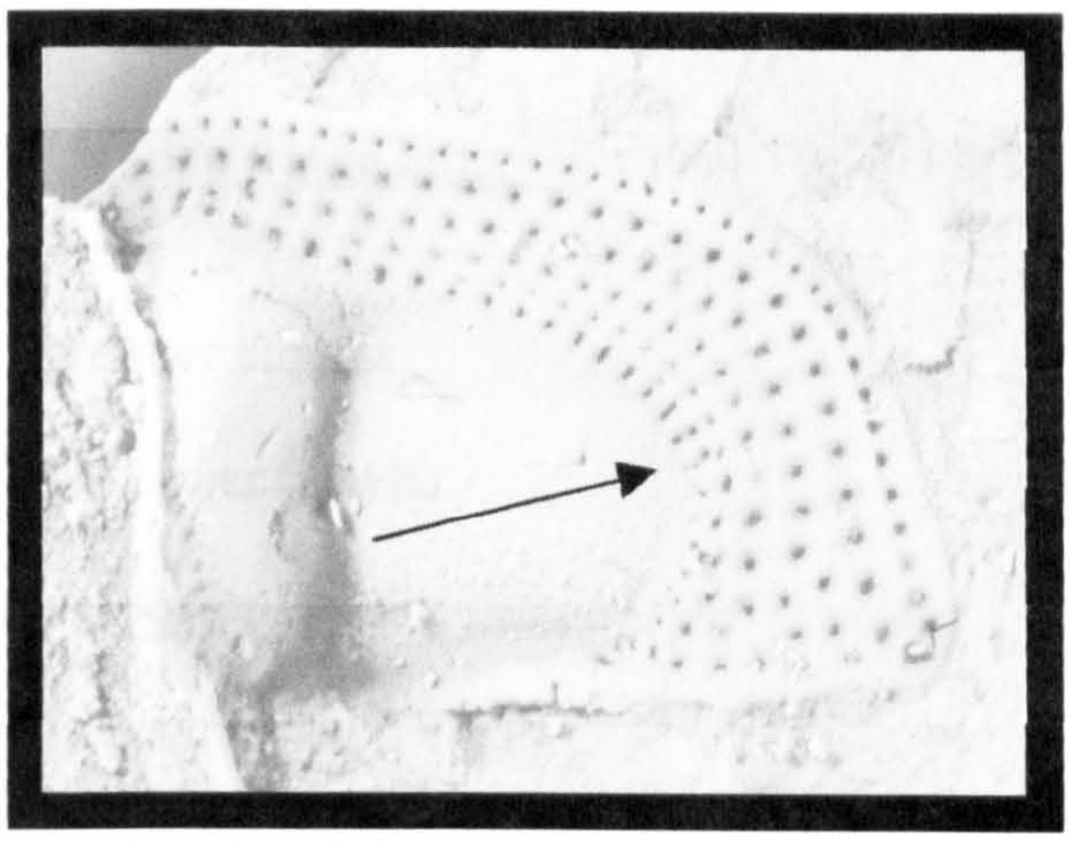
0 - random pits, in some cases such as *Protolloydolithus*, the irregular internal pits are not developed into distinct concentric arcs.

1 - I_3

2 - I_4

3 - I_5

4 - I_6 and higher numbered arcs



Text-Fig. 3.17. *Deanaspis goldfussiigoldfussii* showing I_n cut-off by arc I_5, x8.5.

20. Number of arcs mesially

This count excludes the E and I_n arcs, which are invariably present mesially.

0 - random pits, some species show irregular pit distribution frontally, e. g. *Protolloydolithus ramsayi*.

1 - 1 clear arc (I_1) present in front of the glabella, excluding E and I_n arcs.

2 - 2 clear arcs (I_1, I_2) present in front of the glabella, excluding E and I_n arcs.

Etc.

Fringe inflations.

Fringe inflations are those areas of the fringe where pits are raised to a higher level than the normal fringe surface; an increase in pit diameter may or may not be present. Inflation may occur on one or both lamellae but as some species are only known from either an upper or lower lamella, this is not a character that can be fully coded in all cases. Because of the complex nature of fringe inflations, 12 characters are defined in order to encompass the range of character states.

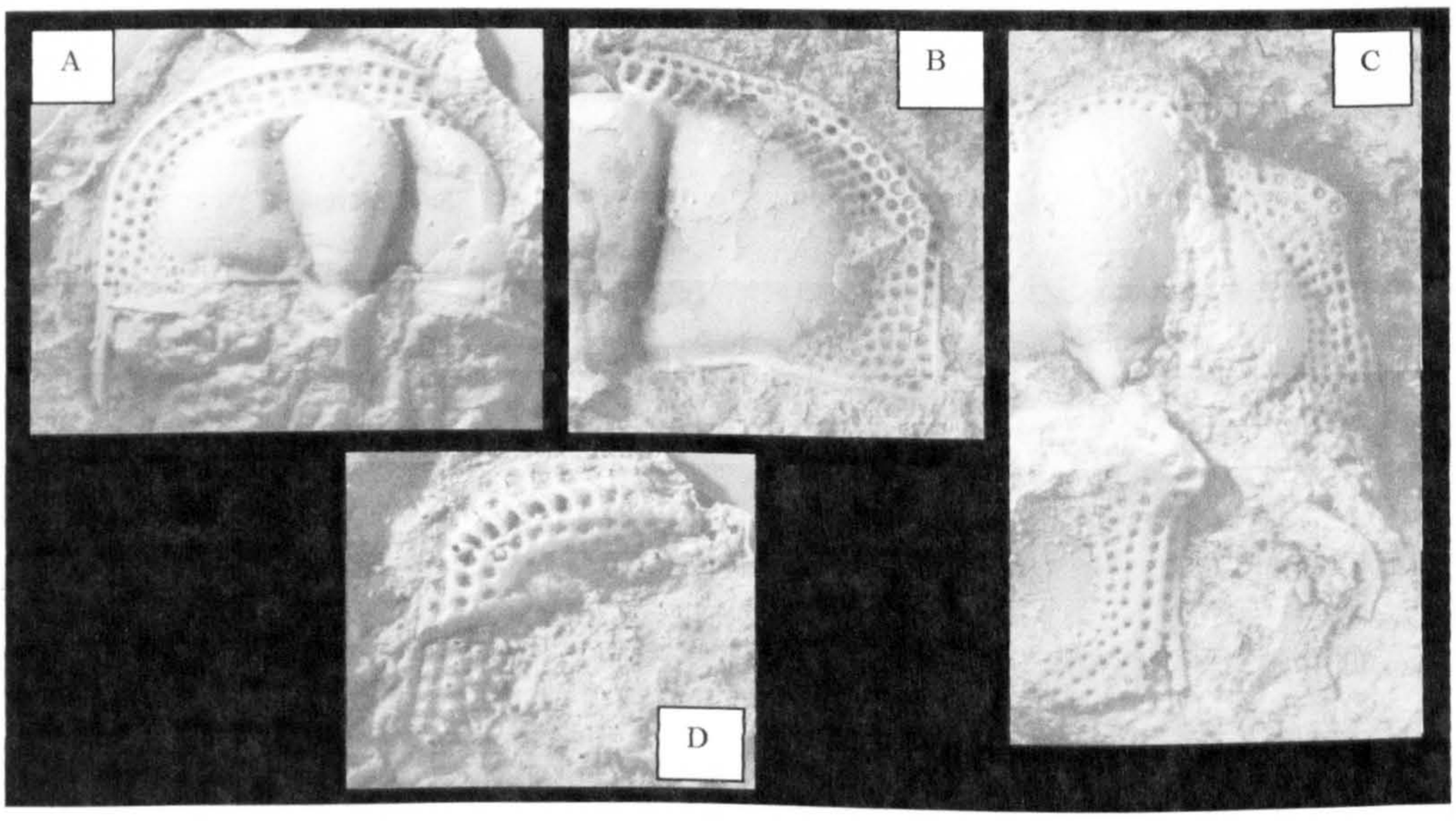
21. Lamellae involved in fringe inflation (Text-Fig. 3.18)

0 – no inflation on either lamella

1 – inflation only on upper lamella

2 – inflation only on lower lamella

3 – inflations on both lamellae



Text-Fig. 3.18. Lamellae involved in inflation shown by A. *Bettonolithus chamberlaini*, no inflation, x5; B. *Marrolithoides simplex* shows inflation only on the upper lamella, x3; C. *Marrolithus* (s. l.) *arenarius* shows inflation only on the lower lamella, x3; D. *Marrolithus* (s. l.) *elegans* has distinct inflations on both the upper and lower lamellae, x2.

22. Location of inflation (Text-Fig. 3.19)

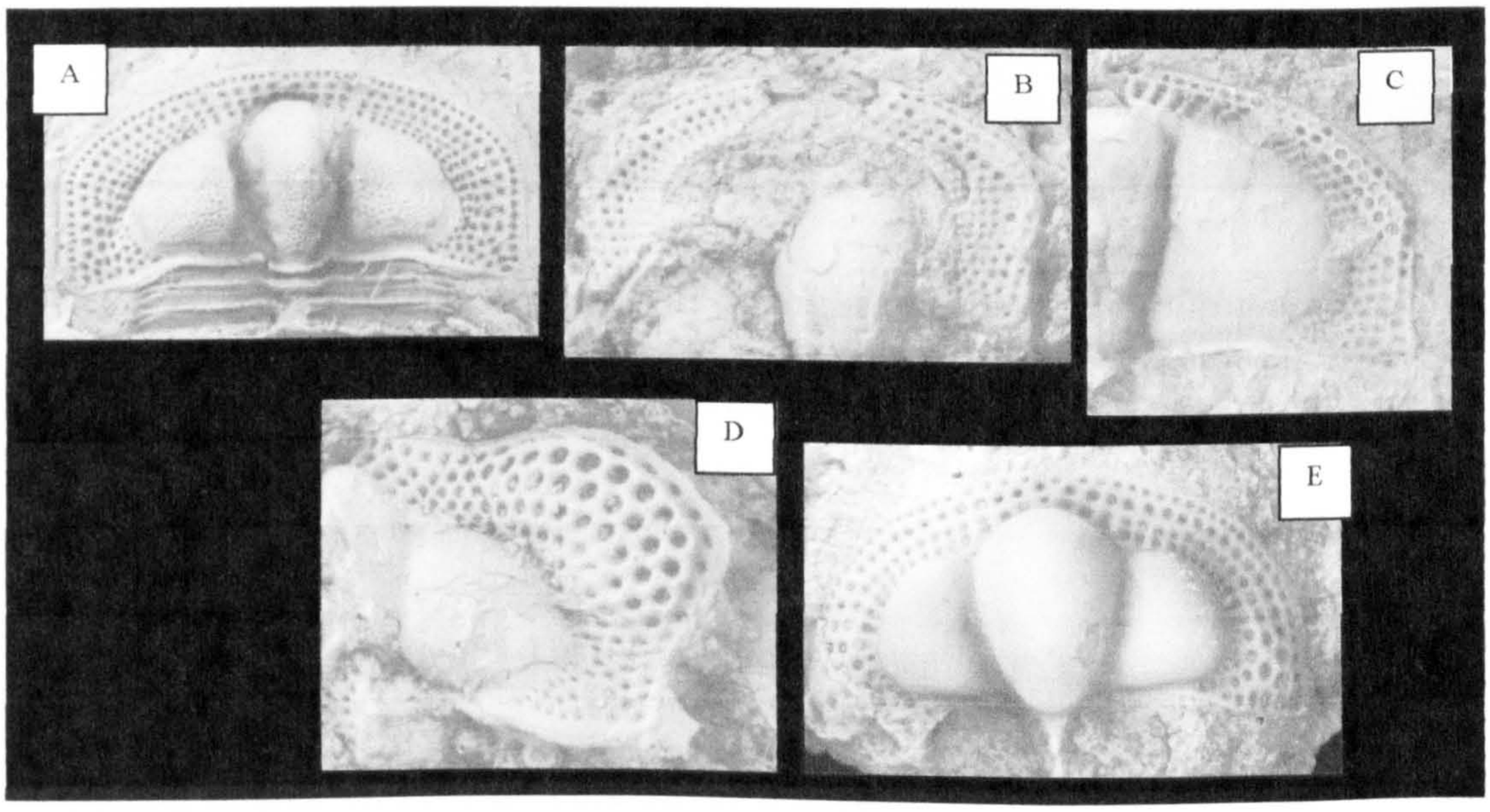
0 - absent

1 - single arc over the majority of the fringe

2 - single arc around lateral area

3 - multiple arcs centred on lateral area of fringe

4 - multiple arcs centred on posterior area of fringe



Text-Fig. 3.19. Specimens showing location of fringe inflation A. *Deanaspis goldfussii goldfussii* possessing no fringe inflation, x5; B. *Hammannaspis paulisper* with a single arc of inflation laterally, x2.5; C. *Marrolithoides simplex* showing only lateral inflation of one arc, x3; D. *Marrolithus favus magnificus* with its multiple arc inflation centred on the lateral area of the fringe, x5; E. *Onnia ultima canthyle* showing multiple arc inflation centred on the posterior area of the fringe, x3.5.

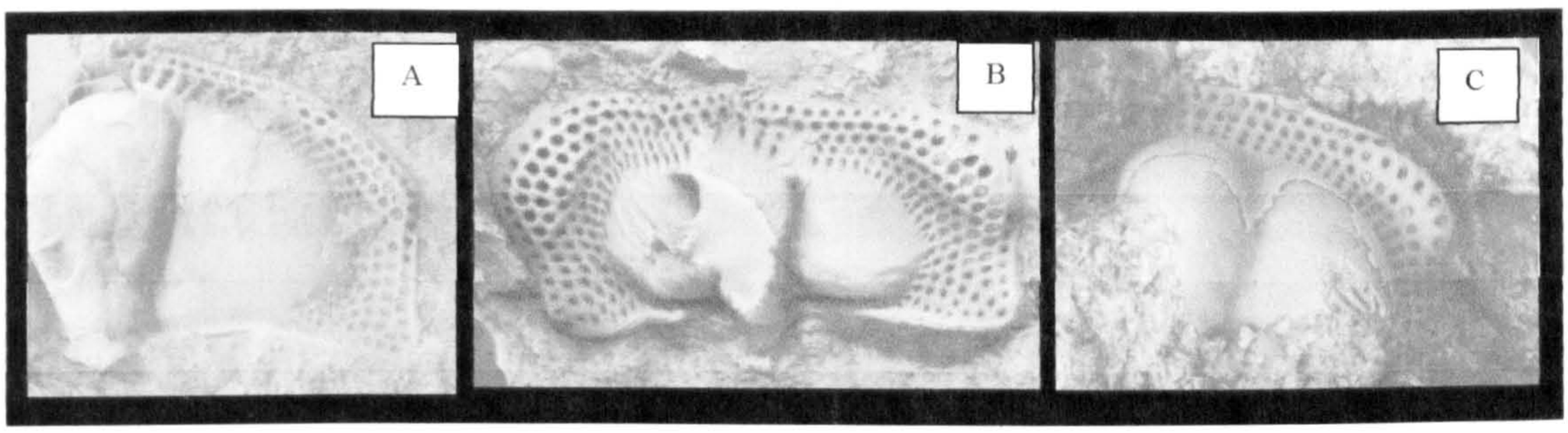
23. Extent of inflation on Upper lamella (Text-Fig. 3.20)

0 – absent

1 – slight inflation - very little height variation between pits affected by the inflation and those on the surrounding fringe.

2 – prominent inflation - pronounced difference in height between pits affected by the inflation and the surrounding fringe.

3 - steep increase in pit height with only one or two pits between the top of the inflation and those pits within the arc not affected by the inflation.



Text-Fig. 3.20. Degrees of inflation: A. slight inflation (*Marrolithoides simplex*), x3. B. prominent inflation (*Marrolithus favus favus*), x3.5. C. steep inflation (*Marrolithus* (s. l.) *elegans*), x3.

24 . Number of arcs involved in the inflation - Upper lamella

Counting all arcs with one or more elevated pit(s):

0 - none

1 - 1

2 - 2

3 - 3

4 – 4

25. E_1 arc pits involved in the inflation - Upper lamella.

0 - E_1 pits not involved

1 - E_1 pits involved

26. Number of I_1 pits involved in the inflation - Upper lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - $\geq$ 11 pits

27. Number of I_2 pits involved in the inflation - Upper lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - $\geq$ 11 pits

28. Number of I_3 pits involved in the inflation - Upper lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - $\geq$ 11 pits

29. Extent of inflation - Lower lamella.

0 – absent

1 – slight inflation - very little height variation between pits affected by the inflation and those on the surrounding fringe.

2 – prominent inflation with pronounced difference in height between pits affected by the inflation and the surrounding fringe.

3 - steep increase in pit height with only one or two pits between the top of the inflation and those pits within the arc not affected by the inflation.

30. The number of arcs involved in the inflation - Lower lamella.

Counting all arcs with one or more elevated pit:

0 - none

1 - 1

2 - 2

3 - 3

4 – 4

31. E_1 arc pits involved in the inflation - Lower lamella

0 - E_1 pits not involved

1 - E_1 pits involved

32. Number of I_1 pits involved in the inflation - Lower lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - ≥ 11 pits

33. Number of I_2 pits involved in the inflation - Lower lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - ≥ 11 pits

34. Number of I_3 pits involved in the inflation - Lower lamella.

0 - 0 pits

1 - 1-4 pits

2 - 5-10 pits

3 - ≥ 11 pits

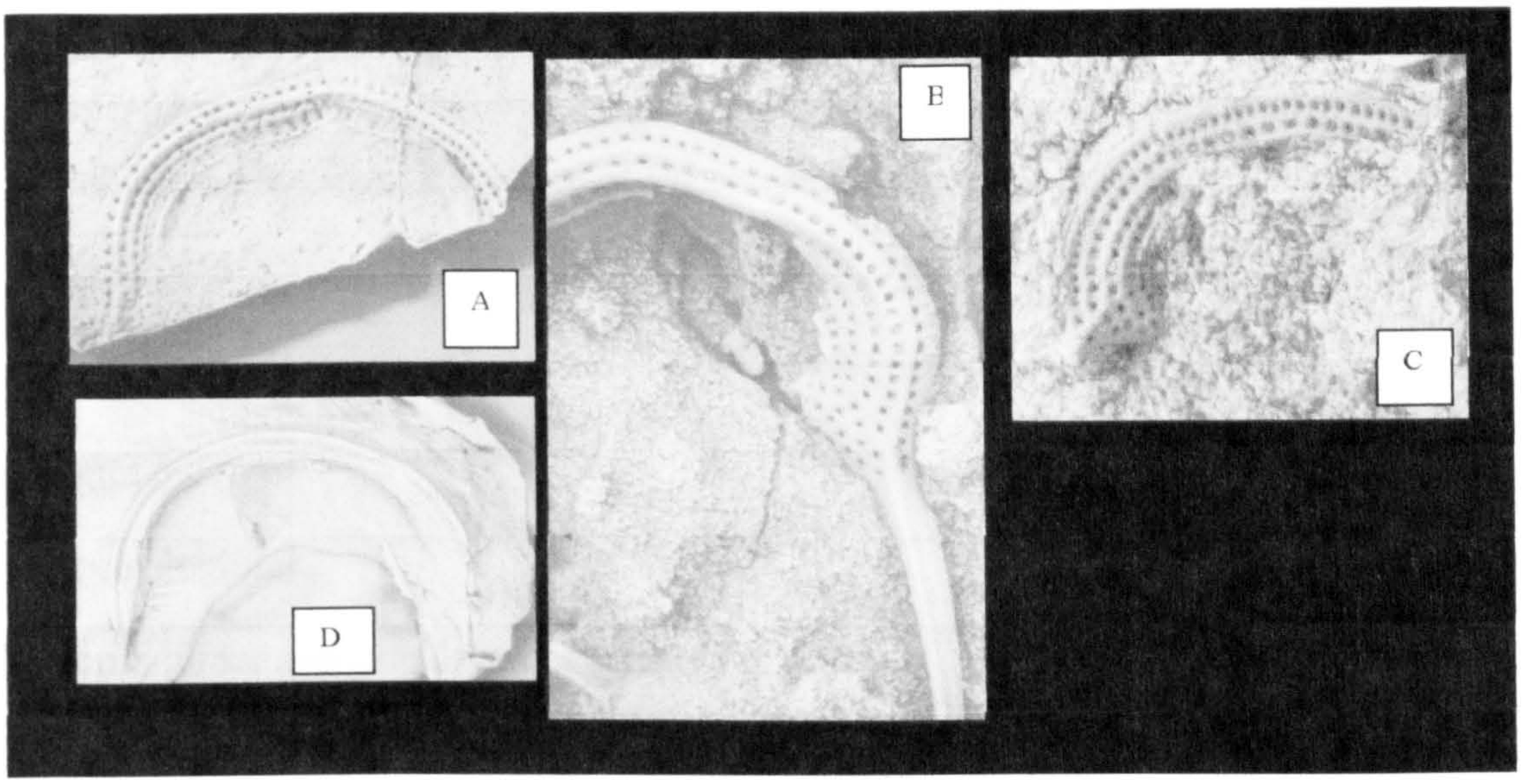
35. Girder - pseudogirder prominence in front of glabella (Text-Fig. 3.21)

0 - girder more prominent than pseudogirder in front of glabella

1 - girder and pseudogirder about equal in prominence in front of glabella

2 - girder less distinct than pseudogirder in front of glabella

3 - neither girder nor pseudogirder prominent in front of glabella



Text-Fig. 3. 21. Various Marrolithinae showing the different types of girder and pseudogirder prominence in front of the glabella. A. *Whittardolithus superstes* showing only a girder frontally, x3.5; B. *Deanaspis goldfussii goldfussii* with subequal girder and first internal pseudogirder frontally, x5; C. *Onnia ultima ultima* with a prominent pseudogirder and no girder frontally, x5; D. *Lloydolithus lloydi* with neither girder nor pseudogirder prominent in front of the glabella, x2.

36. Girder - pseudogirder prominence laterally

0 - girder more prominent than pseudogirder laterally

1 - girder and pseudogirder about equal in prominence laterally

2 - girder less distinct than pseudogirder laterally

3 - neither girder nor pseudogirder prominent laterally

37. Girder - pseudogirder prominence posteriorly

0 - girder more prominent than pseudogirder posteriorly

1 - girder and pseudogirder about equal in prominence posteriorly

2 - girder less distinct than pseudogirder posteriorly

3 - neither girder nor pseudogirder prominent posteriorly

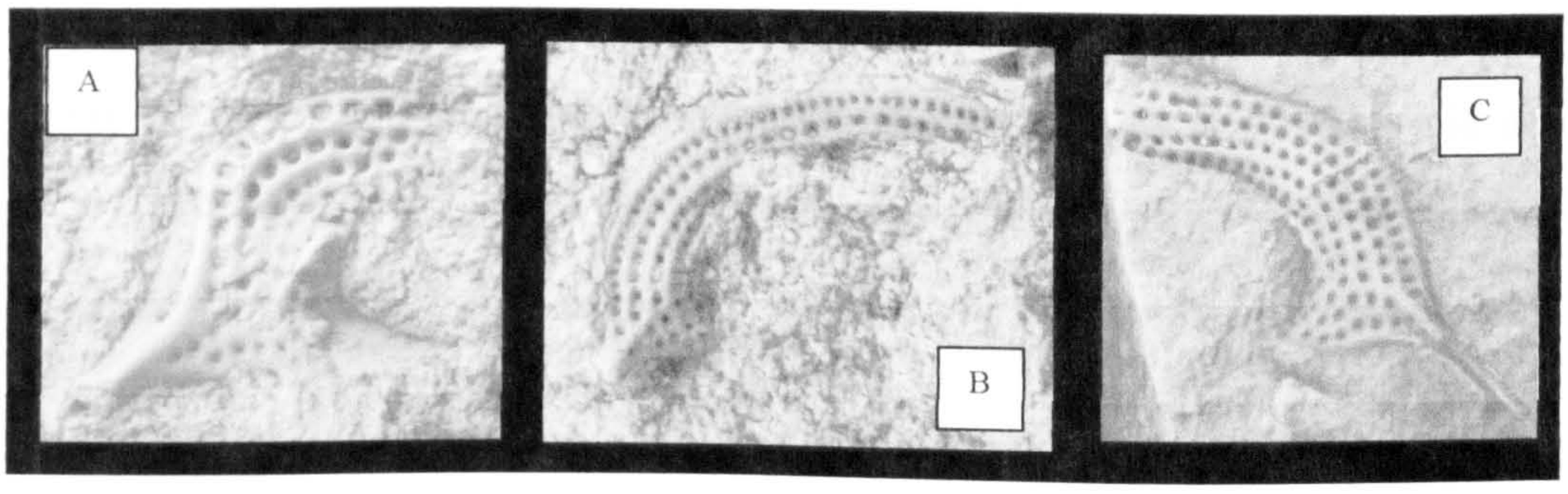
38. The genal spine ridge connection (Text-Fig. 3. 22)

The ridge on the ventral surface of the lower lamella extending from the genal spine may be confluent with the girder or extend further and connect with internal pseudogirders.

0 - girder

1 - pseudogirder

2 - both girder and pseudogirder are connected



Text-Fig. 3.22. Specimens showing ventral ridge; A. *Hammannaspis prima* sp. nov. showing ridge joining girder, x5; B. *Onnia ultima canthyle* sp. nov. with ridge extending to first internal pseudogirder (used by Shaw (1995) as a diagnostic character), x5; C. *Onnia etyma* sp. nov. showing ridge bifurcating to girder and first internal pseudogirder, x4.

3.2.2 Characters not used in the cladistic analysis

These qualitative characters were not used for the cladistic analysis but have been used in earlier diagnoses.

Size

The size of specimens is a variable character that is in part genetic but also reflects on individual's age and possibly local environmental conditions (e.g. nutrient availability).

Reticulation

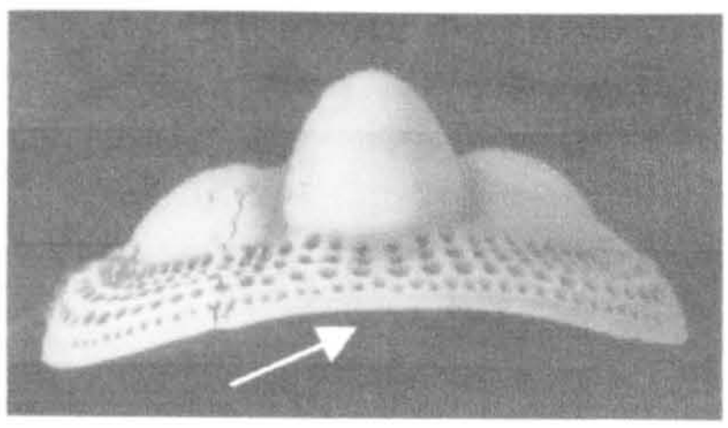
This is generally present on the glabella and genal lobes of juveniles. In larger individuals, reticulation may be absent or present only on the topographic highs of the glabella and genal lobes. Determination of reticulation is also dependent on whether a specimen shows the external surface or is an internal mould. The former may be reticulated, the latter smooth for the came individual. There is also some intraspecific variation in this character and so it was not used for cladistic analysis.

Glabella

The true shape of the glabella is possibly the most difficult morphological character to define, as its outline and elevation can be easily altered during sediment compaction and tectonic deformation. Despite this, it has been used in the past as a diagnostic character for some genera.

Anterior arch (Text-Fig. 3. 24)

The arch was a difficult feature to quantify in uncrushed specimens. Fracture lines radiating outwards across the fringe either side of the glabella are associated with crushed specimens with anterior arches, however it was not possible in such cases to ascertain the size of an arch. As there are many assumptions in the use of this feature in cladistic analysis it was decided to omit it.



Text-Fig. 3.23. An uncrushed silicified *Onnia gracilis* with distinctive anterior arch, x3.

Genal lobe convexity

There are some differences in genal lobe convexity between species but the range is slight and difficult to quantify.

3.3 Method and results

To ascertain those characters that could be used to diagnose each genus, all currently accepted species of Marrolithinae, listed below, were coded. Taxa based on one partial specimen or poor material have not been included, namely *Marrolithus ventriculatus*, *M. scalpriformis* and *Reuscholithus terryi*.

3.3.1 List of analysed taxa

Protolloydolithus ramsayi (Hicks, 1875)

P. reticulatus (Elles, 1940)

P. neintianus Whittard, 1956

P. salax (Rushton and Hughes, 1981)

P. France (a single specimen found in the Armorican Massif, described by Henry *et al.* (1993) as *P.* sp.)

P. Portugal (a single specimen from Portugal, described by Romano 1990)

Bettonolithus chamberlaini (Elles, 1940)

Reuscholithus reuschi Bancroft, 1929*b* [=*R. terryi* from Venezuela]

Costonia ultima (Bancroft, 1949)

C. elegans Dean, 1960

C. arenaria (herein this only refers to Welsh material; Bettley *et al.* (2001 and unpublished thesis 1998) moved *Marrolithus arenarius* to *Costonia* and incorporated Welsh material)

C. a. addisoni (a nomen nudem of Bettley *et al.* (2001) for certain Welsh specimens)

Marrolithus arenarius Whittard, 1958

Marrolithus bilinearis Whittard, 1958

M. craticulatus Whittard, 1958

Marrolithus favus favus (Salter, 1848)

M. f. moderatus Williams, 1948

M. inflatus inflatus Williams, 1948

M. i. maturus Williams, 1948

M. incipiens Williams, 1948

M. magnificus MacGregor, 1963

M. primus Williams, 1948

M. inornatus Whittard, 1956

M. bureaui (Oehlert, 1895)

M. Morocco (previously undescribed material from Morocco)

M. lirellatus MacGregor, 1963

M. ornatus (Sternberg, 1833)

M. paulisper Přibyl and Vaněk, 1969

Marrolithoides anomalis (Williams, 1948)

M. arcuatus Whittard, 1956

M. simplex simplex (Williams, 1948)

M. s. elevata (Williams, 1948)

Deanaspis goldfussii (Barrande, 1846)

D. bedinanensis (Dean, 1967)

D. goldfussii fluminensis Hammann and Leone, 1997

D. laticirrus (Dean, 1967)

D. inferus (Dean, 1967)

D. vysocanensis (Přibyl and Vaněk, 1969)

D. aff. *vysocanensis* Hammann and Leone, 1997

D. ? *novaresei* Hammann and Leone, 1997

D. Morocco (previously undescribed material from Morocco)

D. orthogonius (Dean, 1967)

Onnia superba superba (Bancroft, 1929*b*) (as recognised in Owen and Ingham 1988)

O. s. cobboldi (Bancroft, 1929*b*) (as recognised in Owen and Ingham 1988)

O. s. creta Owen and Ingham, 1988

O. seunesi (Kerforne, 1900)

O. pusgillensis (Dean 1961)

O. superba Bohemia (*Onnia* specimens from Bohemia identified as *O. superba* by Shaw 1995)

O. ultima (Barrande, 1852)

O. gracilis (Bancroft, 1929*b*)

O. grenieri (Bergeron, 1894)

Lloydolithus lloydi (Murchison, 1839)

Whittardolithus inopinatus (Whittard, 1958)

W. instabilis (Hughes, 1971)

W. intertextus (Whittard, 1958)

W. radiatilis (Whittard, 1958)

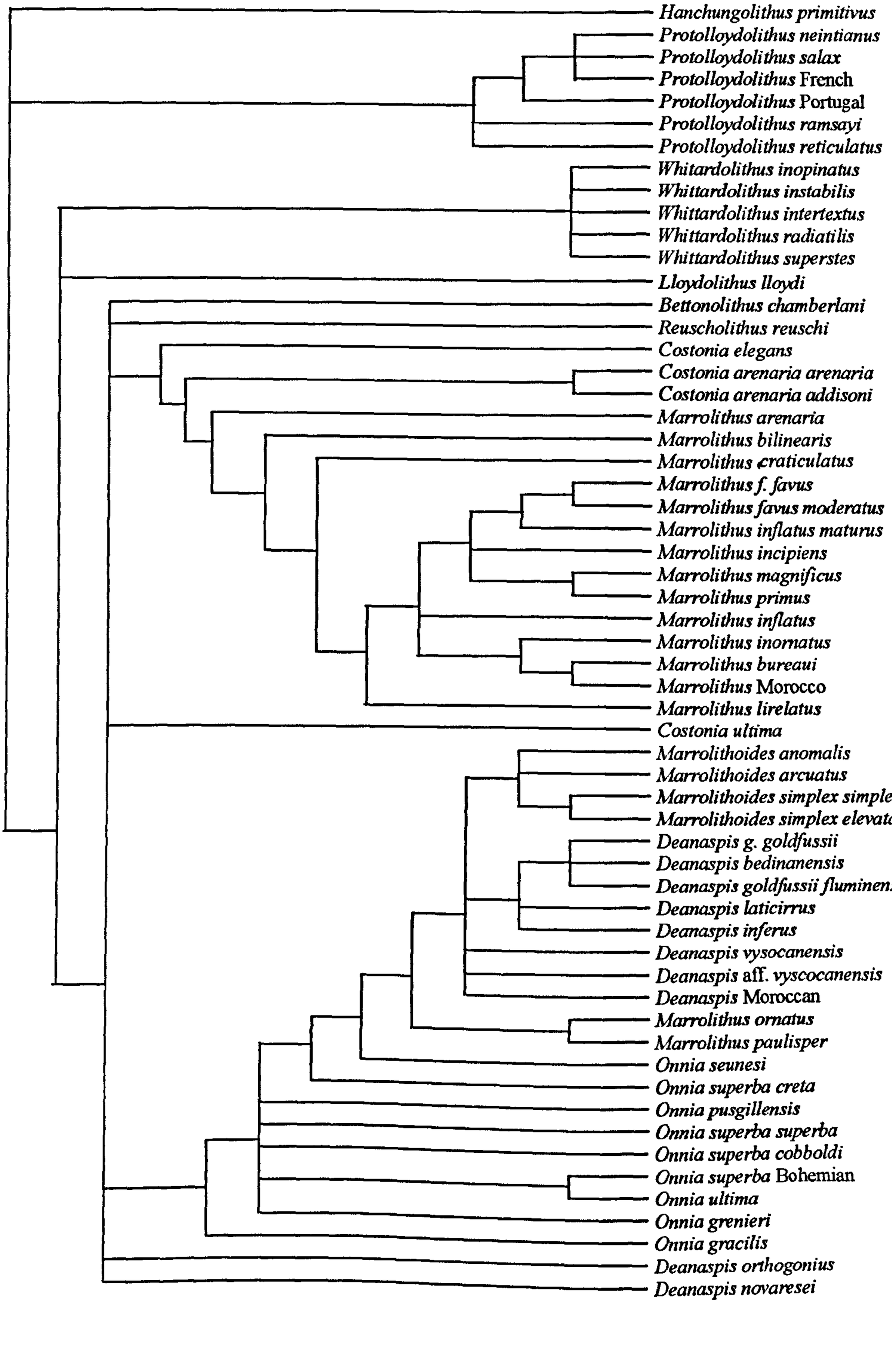
W. superstes (Whittard, 1956)

The character states for the species were tabulated (see Appendix Table 1) and formed the nexus file in PAUP 3.0. The approach used for the cladistic analysis was explicitly typological, each taxon based on one specimen (holotype or lectotype). This strict approach does not reflect the variability in characters seen in most samples but does test the validity of the individual species, *sensu stricto*. Character variability has been taken into account when the resultant branches were analysed (see Systematic Section, Chapter 4). All characters were unordered. The characters used do not show any heterochronic features that would have enabled ordering and the stratigraphical occurrence of taxa was not used in determining possible primitive and derived character states.

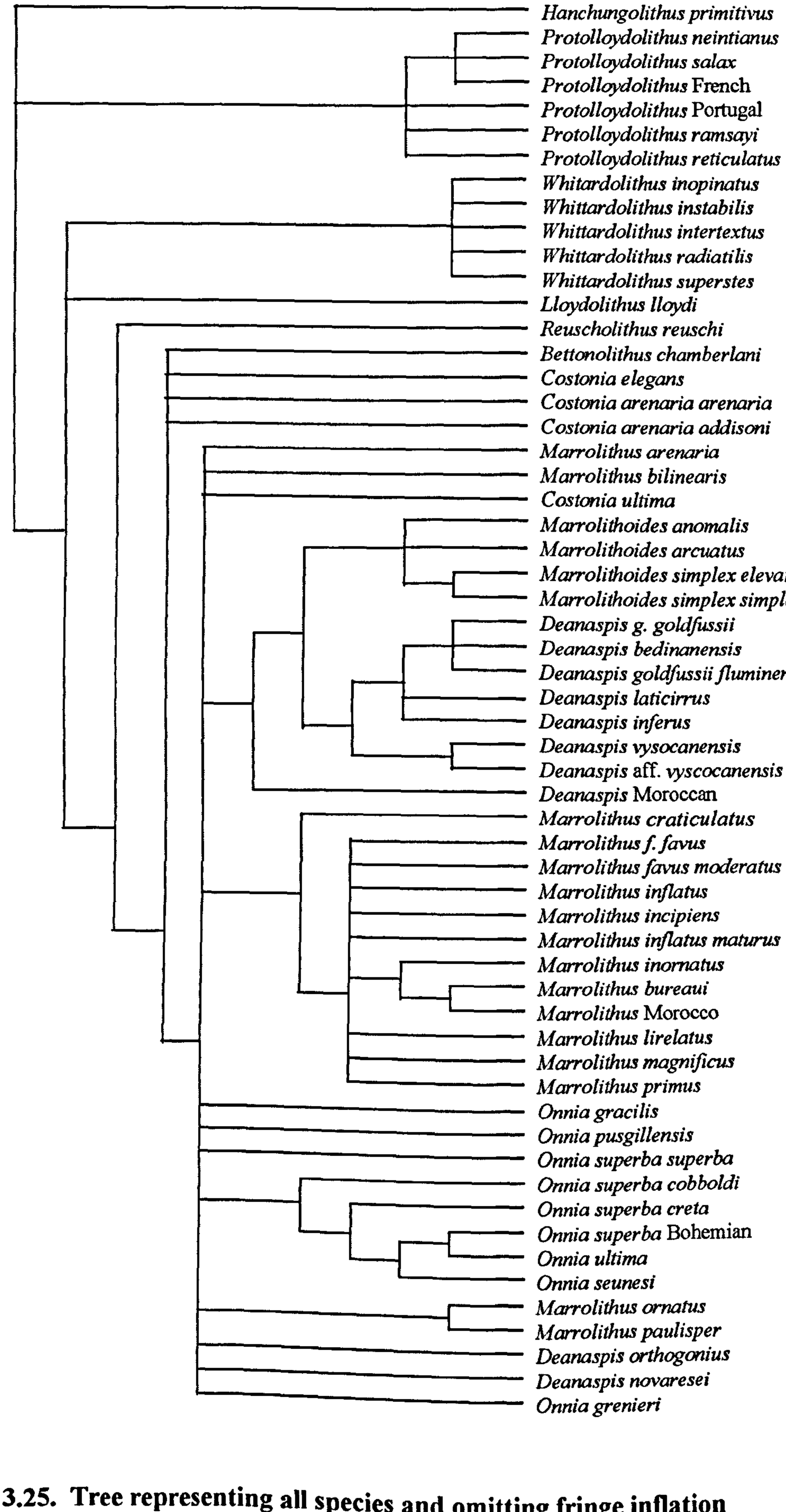
An initial heuristic search was carried out to ascertain the upper limit of tree length. Two exhaustive runs (taking several hours) were undertaken using all the species and all the characters to compare with branch and bound searches (completed within an hour). The final results were the same. *Hanchungolithus primitivus* (Born, 1921) the

probable ancestor of the Marrolithinae was assigned as the outgroup. Confidence in the results was measured using the Consistency Index (CI) (see Section 3.1) generated by PAUP during each analysis. In cases of large numbers of equally parsimonious trees, the strict consensus tree was calculated from the resultant trees. The strict consensus tree only contains those monophyletic groups that are common to all competing trees. Peers (1997) tested whether the order of entry of the taxa affected the final phylogenetic outcome as reported by some workers (e.g. Lespérance & Desbiens 1995). He found the order of display changed but, importantly, the relative ordering of the branches remained the same.

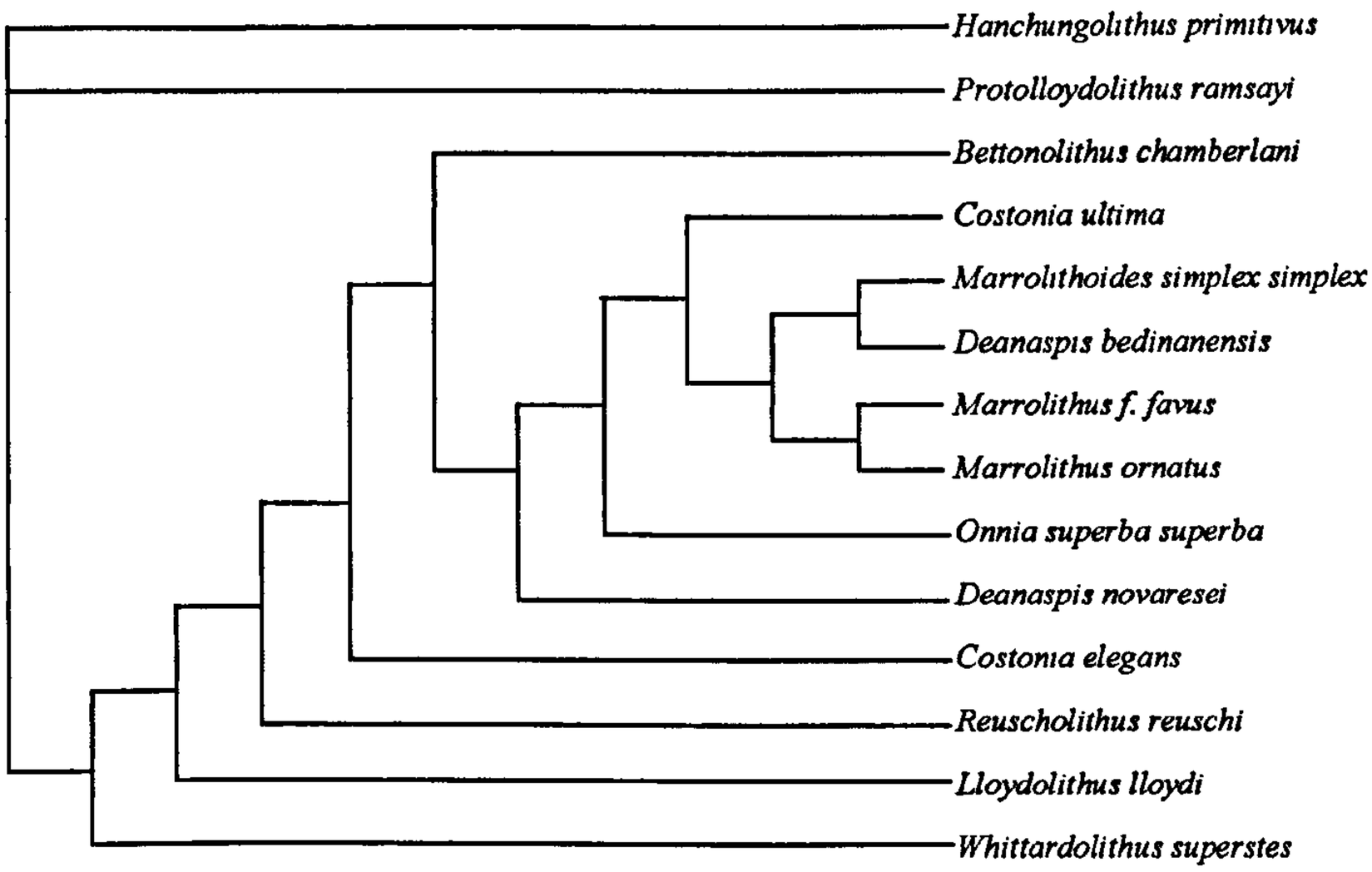
Three cladisitic analyses were carried out. The first contained all species using all characters and produced in excess of two hundred trees of length 214 and a CI of 0.376 (see strict consensus tree Text-fig. 3.24). To test if there was a possibilty of the results being artificially weighted by those taxa not showing fringe inflation appearing to be closely associated, a second analysis was carried out containing all species but with the characters describing the details of any fringe inflation (i. e. characters 23-34) omitted. This analysis produced over two hundred trees of length 139 and a CI of 0.367 (see strict consensus tree Text-fig. 3.25). The third cladistic analysis contained only the type species and problematical taxa highlighted from the first two cladograms and this analysis produced a single tree of shortest length 101 and CI of 0.58 (see Text-fig. 3.26).



Text-fig. 3.24 Cladogram (length 214, CI 0.376) showing most marrolithine species (see above for details of names) and new material from Morocco.



Text-Fig 3.25. Tree representing all species and omitting fringe inflation characters (23-34).



Text-Fig. 3. 26. The cladogram resulting from the type species (as hitherto understood) and problematical taxa. One tree of shortest length 101 and C. I. of 0.58.

Many species group neatly together in both species cladograms (Text-Figs 3.24 and 3.25), such as those ascribed to the genera *Protolloydolithus*, *Whittardolithus*, *Marrolithoides*, *Deanaspis* and *Marrolithus*. These monophyletic groups do not present any difficulties in their generic definitions and give support to the synonymies detailed in the Systematics Chapter (Chapter 4). The monospecific genera *Bettonolithus*, *Lloydolithus* and *Reuscholithus* generally plot as sister groups and at low nodal positions not related to their stratigraphical positions but all three are less derived on all cladograms than *Marrolithus*, *Marrolithoides*, *Onnia* and *Deanaspis* (Text-Figs 3.24, 3.25, 3.26). *Deanaspis* and *Marrolithoides* appear as sister groups on both cladograms and *Deanaspis* is better resolved on the cladogram without the inflation details (Text-Fig. 3.25). Similarly, on the type species cladogram (Text-fig 3.26) both *Deanaspis* and *Marrolithoides* appear as sister groups. The next shortest tree length (102) of the type species cladogram resulted in 43 trees, the strict consensus tree showed only *Marrolithoides* and *Deanaspis* as a dichotomy and all other taxa were unresolved.

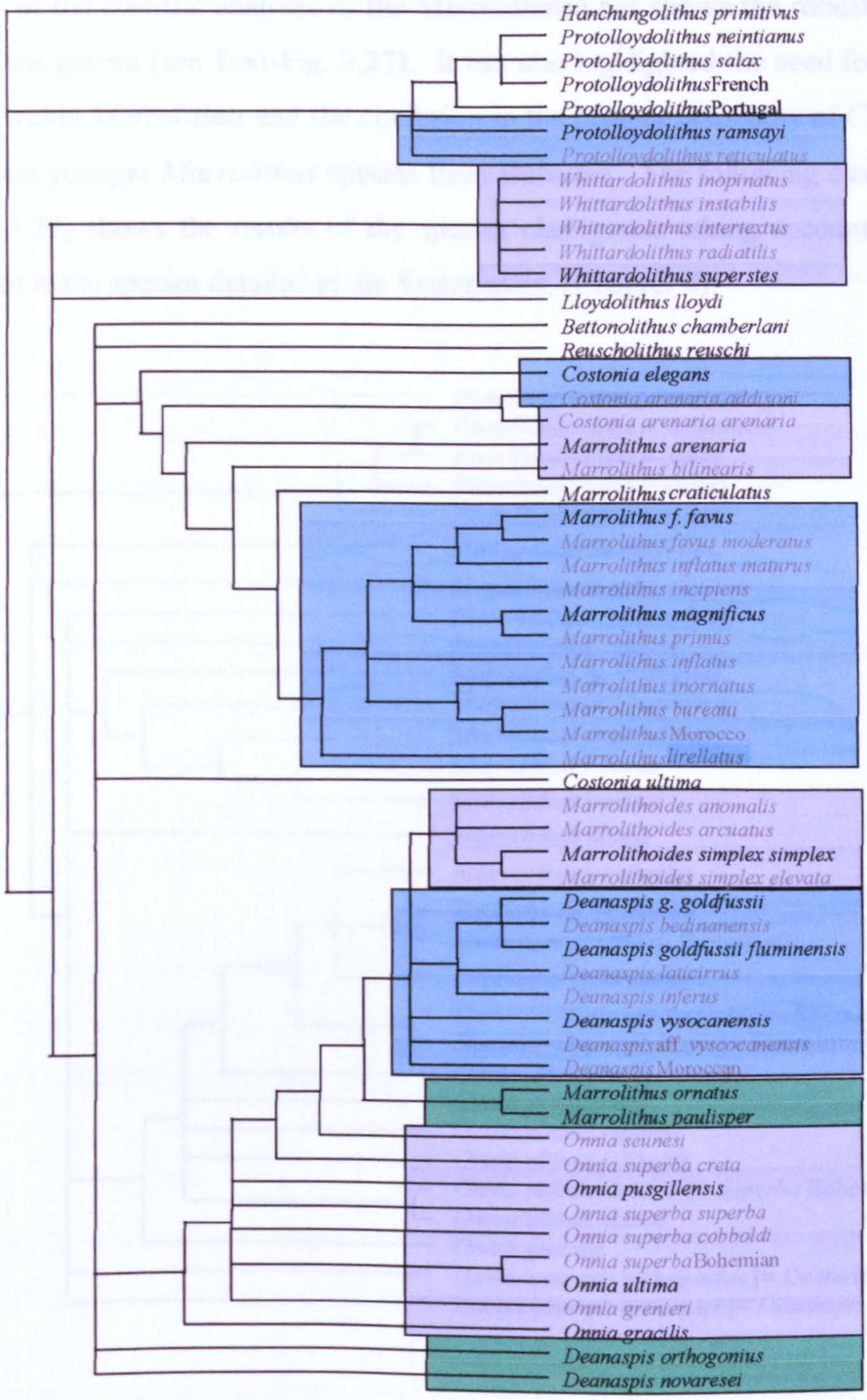
On both species cladograms (Text-Figs 3.24 and 3.25) *Onnia* appears paraphyletic to the extent that the Avalonian *Onnia superba* subspecies are separated at different nodes. Given the very strong overlap between population samples of these subspecies (Owen and Ingham 1988), the cladistic analysis provides no useful clarification of relationships within the genus. In the cladogram showing all species and all characters (Text-Fig. 3.24) *Onnia grenieri* and particularly *O. seunesi* are poorly constrained within the *Onnia* group. Within the cladogram omitting the inflation characters *O. grenieri* remains separate. *Onnia grenieri* and *O. seunesi* were both coded as for *Onnia* with a more prominent pseudogirder the girder frontally, however, since the cladistic analysis was carried out it has become apparent that the girder is equally strong in both species and this discrepency was shown on the cladograms by the lability of these taxa and lack of resolution to the *Onnia* clade. Therefore, *Onnia grenieri* and *O. seunesi* must be reassigned to *Deanaspis*.

Onnia has hitherto been interpreted as being derived from *Deanaspis* on the basis of the girder and pseudogirder development (for example, Hughes *et al.*, 1975). The results of the strict consensus cladograms for the analysis of all species show *Onnia* as less derived than *Deanaspis*. The two hundred trees resulting from the analysis for all species and all characters are composed of around 75 percent with *Deanaspis* more derived than *Onnia* and the remaining trees placed the two genera as sister groups. None of the trees showed *Deanaspis* as ancestral to *Onnia*. All characters used in the cladistic analysis were unordered so as not to influence the phylogeny. A test run was made to see if the positions of *Deanaspis* and *Onnia* changed if character 35, detailing the prominence frontally of the girder and pseudogirder, was ordered from girder through to pseudogirder dominant frontally in sequence. The results of this run did not alter the positions of the two genera. It is probable therefore that they do not represent a direct linear relationship.

The cladogram with all species and all characters (Text-Fig. 3.24) show all of the Avalonian "species" ascribed to *Marrolithus*, including the Welsh material termed "*Costonia*" *arenaria* subspecies by Bettley *et al.* (2001 and Bettley 1998, unpublished Ph. D. thesis), together with *M. bureaui* and the Moroccan *M.* sp. lie within a holophyletic clade which is internally fairly well differentiated. However,

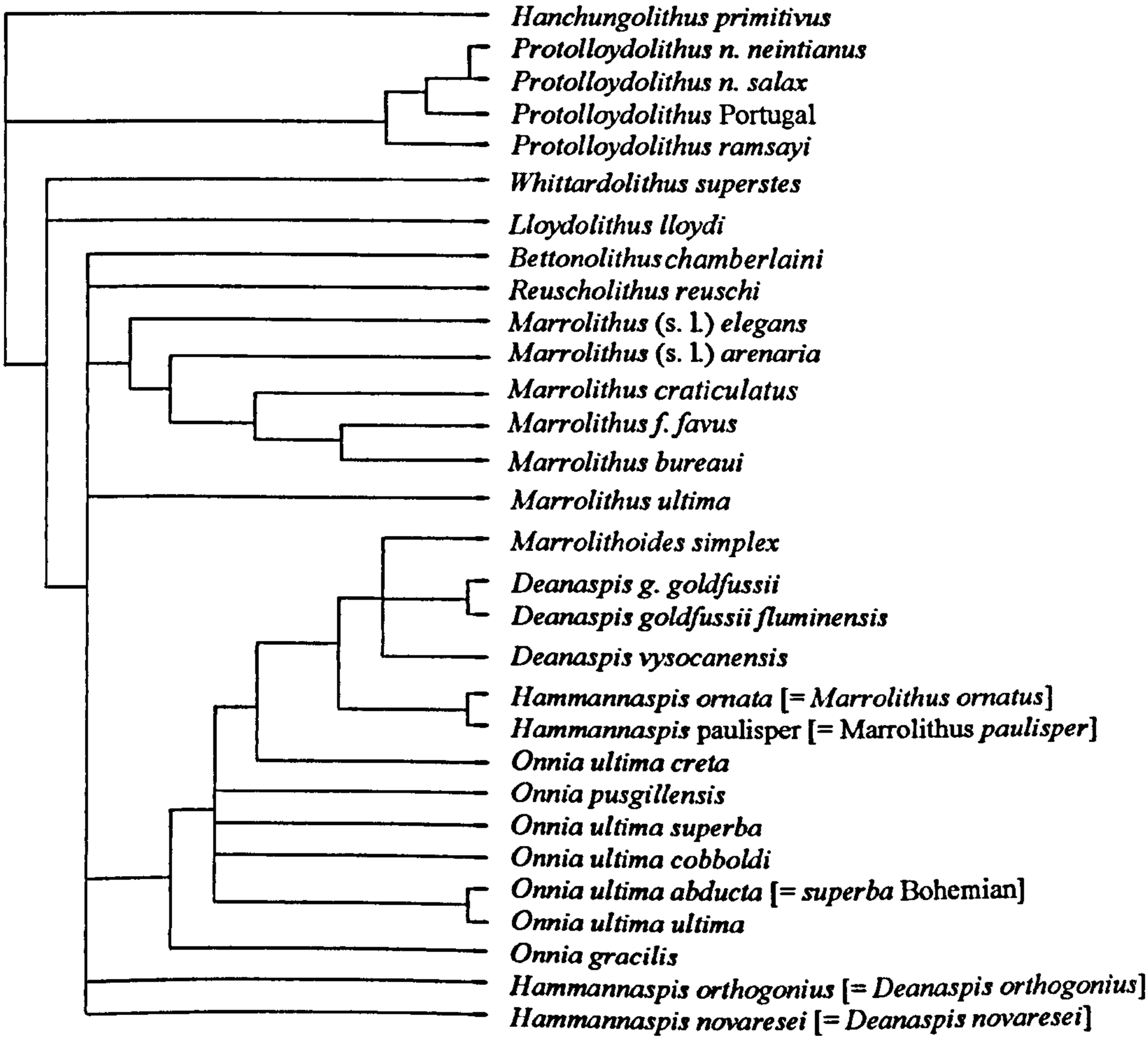
the cladogram based on all species and omitting the detailed fringe inflation characters (Text-Fig. 3.25) shows a more limited holophyletic *Marrolithus* clade with little internal resolution. This clearly suggests major synonymy within the clade is required (see Systematics Chapter, 4). *Marrolithus arenarius* (and the Welsh material termed *Costonia arenaria arenaria* and *C. a. addisoni*) and *M. bilinearis* are excluded from the holophyletic *Marrolithus* clade on this cladogram. They are here considered to be sufficiently close to *Marrolithus* to be termed *Marrolithus* (sensu lato). The same applies to *Costonia ultima* (the type species of *Costonia*) and *C. elegans* which are also very labile when all three cladograms are compared (Text-Figs 3.24, 3.25, 3.26). This lability highlights the problems with their current classification. Moreover, the present study shows that samples containing *Marrolithus arenarius* (Whittard), *Costonia arenaia* (sensu Bettley) and *Marrolithus bilinearis* (Whittard) [= *Marrolithus* (s. l.) *arenarius*] and *Costonia elegans* (Dean) and *Costonia arenaria addisoni* (Bettley *nomen nudum*) [= *M.* (s. l.) *elegans*] show considerable temporal and spatial variation (see Section 6.1).

Marrolithus ornatus, a much younger Bohemian species than the Avalonian *Marrolithus* appears in different places on each of the three cladograms. *Marrolithus ornatus* is the sister group of the Bohemian species, *M. paulisper* but the two are not associated with the *Marrolithus* clade. On the type species cladogram *Marrolithus ornatus* and *Marrolithus favus* are sister groups, their association is based on fringe inflation and girder prominence on the lower lamella. The cladistic analyses have highlighted a phylogenetic "distance" between the Bohemian and Avalonian *Marrolithus*. *Deanaspis orthogonius* and *D. novaresei* always appear as sister taxa separate from the *Deanaspis* clade. These two species are associated with *Marrolithus ornatus* and *M. paulisper* on the cladogram without fringe inflation characters. These four species are herein placed in *Hammannaspis* gen. nov. (see Systematics Section, Chapter 4).



Text-Fig. 3.27. Cladogram showing revised synonymy of the Marrolithinae. Species not synonymized remain in black type, *P. salax* is regarded herein as a subspecies of *P. neintianus*, *P.* French is considered to be a hanchungolithine and the single specimen from Portugual is placed in *P.* (s. l.). *Costonia ultima* is reassigned to *Marrolithus*. The blue and purple boxes contain species (in grey type) that have been synonymized herein with those species in black type. *M. magnificus* is regarded as a subspecies of *M. favus favus*, *Onnia* and *Deanaspis* contain a number of retained species, *D. vysocanensis* is here synonymised with *D. pongerardi*. The two green boxes contain *Hammannaspis* gen.nov.

The results of the cladistic analyses of the Marrolithinae has shown the robust nature of most of the genera (see Text-Fig. 3.27). It has also highlighted the need for major synonomy within *Marrolithus* and the confusion in the present taxonomy of *Costonia* and the much younger *Marrolithus* species from Bohemia. The following cladogram (Text-Fig. 3.27) shows the results of the species cladograms taking account of the synonymy of many species detailed in the Systematics, (Chapter 4).



Text-Fig. 3.28. Cladogram showing revised synonymy of genera, species and subspecies. Note *Deanaspis vysocanensis* represents *D. pongerardi*, into which it has been synonimsed

Character state changes at the basal nodes of generic clades can be used as diagnostic characters. These include unique characters for some genera and other characters that collectively can be used to diagnose each genus. Some characters that appeared

unique to a taxon on the tree below based on type species show variation within the genus itself and therefore could not be used.

The following lists the diagnostic characters of the various genera, those unique to the genus are underlined:

Protolloydolithus - Preglabellar field; fringe:lobe ratio of 1:<0.4; no occipital spine; poor radial arrangement of pits; E_1 pits much larger than other pits; moderate number of F pits (~20).

Bettonolithus - Fringe:lobe ratio of 1:>0.6; posterior margin extension; sulcate pits; occasionally shows E_2 pits frontally; moderate number of F and irregular pits.

Marrolithoides - Fringe:lobe ratio of 1:1.23; moderate number of F pits; slight elevation in single arc of pits laterally.

Deanaspis - Fringe:lobe ratio of 1: 0.41-0.59; moderate number of F and irregular pits; slight inflation in single arc over most of fringe; pseudogirder as well developed as the girder frontally; pseudogirder channel leads to genal spine ridge.

Marrolithus - Fringe:lobe ratio of 1: 0.41-0.59; width of I_1 pits increase to a maximum at the lateral area of fringe; low number of F pits; multiple arc pits inflated at lateral area of the fringe; I_2 pits involved in inflation.

Hammannaspis - Fringe:lobe ratio of 1: 0.35-0.60; width of I_1 arc pits remain constant; I_1 arc elevated along fringe; low number of irregular and F pits

Omnia - Fringe:lobe ratio of 1: 0.41-0.59; width of I1 pits increase to a maximum at the posterior of fringe; low number of F pits; pseudogirder more dominant than the girder frontally.

Reuscholithus - Fringe:lobe ratio of 1:>0.6; posterior margin extension; poor radial alignement of pits; E2 pits present; high number of F and irregular pits.

Lloydolithus - Preglabellar field; fringe:lobe ratio of 1:>0.6; large genal prolongation; E2 complete; high number of F and irregular pits; 6 or more arcs mesially.

Whittardolithus - Preglabellar field; fringe:lobe ratio of 1:>0.6; genal prolongation; sulcate pits; high number of F and irregular pits.

4 SYSTEMATICS

Samples used for this study are from museum collections prefixed as: Hunterian Museum, University of Glasgow (GLAHM); The Natural History Museum, London (BNHM); British Geological Survey collections, Keyworth (BGS); Sedgwick Museum, University of Cambridge (SM); University of Oxford (OU); Moroccan Geological Survey (MGS); Czech Geological Survey (UUG); Czech National Museum (NM) Museum of Comparative Zoology at Harvard University (MCZ); Palaeontological Institute of the University of Modena, Italy (IPUM)

Family TRINUCLEIDAE Hawle and Corda, 1847

Diagnosis. Bilamellar cephalic fringe possessing numerous opposed pits on external surfaces. The dorsal inframarginal suture becoming dorsal along the posterior margin of the fringe. Thorax consists of six segments. with distal extremities of pleurae deflected downwards. Subtriangular pygidium and posterior and lateral margins deflected nearly vertically donwards.

Subfamily MARROLITHINAE Hughes, 1971

Emended Diagnosis. E, I and F pits well developed. In cut-off laterally by adjacent arc. Extreme pit enlargement commonly associated with fringe swellings. Glabella clavate with small deep basal lateral glabellar furrows.

Type genus. Marrolithus Bancroft, 1929.

Distribution. Llanvirn to Caradoc of Wales and the Welsh Borderland; upper Caradoc to lower Ashgill of Northern England and Sardinia; upper Llanvirn to middle Caradoc of France and Portugal; Caradoc of Spain, Turkey and Central Asia; upper Llanvirn to Ashgill of Bohemia and Morocco.

Remarks. The Marrolithinae have been used as zonal fossils (Bancroft, Bettley) but little has been done to clarify their taxonomy since Hughes *et al.* (1975). The phylogeny proposed by Hughes *et al.* was the original starting point for the cladistic analysis herein. Hughes (1979) and Owen and Ingham (1988) have attempted some taxonomic clarification of the subfamily but little has been done on the variation of morphology within species both spatially and temprally, until now.

Genus **MARROLITHUS** Bancroft, 1929*b*

[= *Costonia* Whittard, 1956]

Type species. *Trinucleus ornatus* var. *favus* Salter, 1848. Original designation by Bancroft 1929. Mydrim Limestone, lower Caradoc Series, Aurelucian Stage, Costonian Substage, *gracilis* Biozone from the road cutting between Stonyford and Pant-y-Gorphyws (SN 12061613), 1.6 km north of Narberth, Pembrokeshire, Wales.

Emended Diagnosis. Fringe to genal lobe ratio, 1:>1. Fringe markedly subquadrate. Variably developed anterolateral inflations, bearing enlarged pits affecting lower and/or upper lamellae and involving a variable number of I arcs and, in some taxa, pits of E_1. Girder most prominent anteriorly; first and second internal pseudogirders only developed anterolaterally, if at all present. Girder list only present anterolaterally in association with inflated areas. In arc is terminated by arc I_4 or I_5.

Remarks. Williams (1948), Whittard (1956) and MacGregor (1963) employed a strict typological approach to *Marrolithus* classification, which has led to a plethora of "species" names. As early as 1848, however, Salter recognised that some population samples show morphological variation and that small differences were not necessarily sufficient for recognition of additional species. Salter noted the distinctive ranges in variation of the marrolithine herein termed *Hammannaspis ornata* (Sternberg, 1833) from Bohemia and *Marrolithus favus* (Salter, 1848) from Shelve and regarded the latter as a subspecies of the former. Bancroft (1929*b*) established his genus *Marrolithus* for specimens showing a rectangular head-shield, particularly characterised by the abrupt antero-lateral angulation of the cephalic margin. Williams (1948) proposed three "natural" groups (subgenera) for the marrolithines and emended Bancroft's generic diagnoses to include trinucleids with a clavate glabella, only one row of pits external to the girder, and with a sharply angulated border. *Marrolithus sensu stricto* specimens were only those showing a variable area of fringe inflation associated with enlarged pits developed at the anterolateral angle. The other two groups comprised species of *Marrolithoides* and *Telaeomarrolithus* (the latter now known to be a trinucleine, see Hughes *et al.*, 1975, pp. 556-7).

Subsequent workers have based the specific diagnoses of *Marrolithus* on the variably developed fringe inflations (Whittard 1956, Dean 1960, Hughes *et al.* 1975, Shaw 1995, Addison 1974 (unpublished Ph.D. thesis) and Bettley 1998 (unpublished Ph.D. thesis). The nomenclature of the swollen area established by Williams (1948) was criticised by Whittard (1956) who, nevertheless, was unable to provide a less subjective terminology. Although Williams stated that pits on the slopes of the swollen areas should not be included in the pit count for the swollen areas, in the present study it has been found necessary to include pits some distance down the slopes to arrive at the counts obtained by both Williams and Whittard. Williams (1948) redescribed *M. favus* and erected five new species and subspecies from the Llandeilo district of South Wales (*M. favus moderatus*, *M. inflatus*, *M. inflatus incipiens*, *M. inflatus maturus* and *M. primus*), all based of small differences in fringe inflation. Whittard (1956) described six new species from the Shelve area of Shropshire (*Marrolithus arenarius*, *M. bilinearis*, *M. craticulatus*, *M. inornatus*, *M. scalpriformis* and *M. ventriculatus*), all similarly based on variations in fringe inflation. A latex cast of the holotype of *M. primus* Williams (1948), however, reveals multiple arc inflation on the upper lamella whereas the species diagnosis stated that it does not display any inflation.

The following species are here placed in *Marrolithus*. Nevertheless, to show the slight uncertainty in the cladistic relationships of some taxa these are provisionally placed in *Marrolithus* (sensu lato) :

Species and subspecies recognized herein:

Marrolithus favus favus (Salter, 1848)

Marrolithus favus magnificus (MacGregor, 1963)

Marrolithus craticulatus Whittard, 1956

Marrolithus (sensu lato) *ultimus* Bancroft, 1949 (previously assigned to *Costonia*)

Marrolithus (sensu lato) *arenarius* (Whittard, 1958)

Marrolithus (sensu lato) *elegans* (Dean, 1960) (previously assigned to *Costonia*)

Distribution. *Marrolithus* was a widespread genus in the Llanvirn and Lower Caradoc of western and central Europe and North Africa. It ranges through south, southwest and north

Wales and Shropshire (the Welsh Basin and its margins) and is also known from the Armorican Massif, Iberia, Bohemia, Morocco and Venezuela (see Hughes et al., 1975, p. 571). The occurrence of *Marrolithus* in the Builth district south Wales is the oldest record of the genus, albeit only as a rarity.

Marrolithus favus favus (Salter, 1847)

Plate1, Figs 1-8; Text-Fig. 4.1-3

1847 *Trinucleus ornatus* var. *favus* Salter; p. 254.

1848 *Trinucleus ornatus* var. *favus* Salter; Salter, p. 350, pl. 9, fig. 3.

1895 *Trinucleus Bureaui* Ohlert, pp. 299-336, p. 1, figs 1-15, pl. 2, figs 16-24.

1929*b* *Marrolithus favus* (Salter); Bancroft, p. 77.

1948 *Marrolithus favus* (Salter); Williams, p. 70, pl. 6, fig. 9.

1948 *Marrolithus favus moderatus* Williams; p. 73, pl. 6, fig. 8.

1948 *Marrolithus favus moderatus* Williams; Whittard, p. 57, pl. 7, fig. 14.

1948 *Marrolithus inflatus* Williams; p. 74, pl. 6, fig. 3.

1948 *Marrolithus inflatus* var. *incipiens* Williams; p. 77, pl. 6, fig. 2.

1948 *Marrolithus inflatus* var. *maturus* Williams; p. 75, pl. 6, fig. 4.

1948 *Marrolithus primus* Williams; p. 78, pl. 6, fig. 1.

1956 *Marrolithus favus* (Salter); Whittard, p. 55, pl. 7, figs 6-13.

1956 *Marrolithus inflatus* Williams; Whittard, p. 55, pl. 7, fig. 5.

1956 *Marrolithus inflatus* var. *maturus* Williams; Whittard, p. 55, pl. 7, figs 2-4.

1956 *Marrolithus inornatus* Whittard; p. 58, pl. 8, figs 1-4.

1956 *Marrolithus scalpriformis* Whittard; p. 62, pl. 8, figs 14-15.

1956 *Marrolithus* cf. *anomalis* (Williams); Whittard, p. 59. pl. 7, fig. 15.

1963 *Marrolithus inflatus maturus* Williams; MacGregor, p. 799, pl. 117, fig. 4.

1963 *Marrolithus favus* (Salter); MacGregor, p. 799, pl. 117, figs 5-11.

1963 *Marrolithus lirellatus* MacGregor; p. 802, pl. 116, figs 15,17-21.

1971 *Marrolithus* sp.; Hughes, pp. 168,169, pl. 14, figs 6, 7.

1975 *Trinucleus ornatus* var. *favus* Salter; Hughes *et al.*, p. 571.

1975 *Marrolithus favus moderatus* Williams; Hughes *et al.*, p. 571.

1975 *Marrolithus inflatus* Williams; Hughes *et al.*, p. 571.

1975 *Marrolithus inflatus incipiens* Williams; Hughes *et al.*, p. 571.

1975 *Marrolithus inflatus maturus* Williams; Hughes *et al.*, p. 571.

1975 *Marrolithus primus* Williams; Hughes *et al.*, p. 571.

1975 *Marrolithus inornatus* Whittard; Hughes *et al.*, p. 572.

1975 *Marrolithus scalpriformis* Whittard; Hughes *et al.*, p. 572.

1975 *Marrolithus lirellatus* MacGregor; Hughes *et al.*, p. 572.

1975 *Marrolithus* cf. *favus*; Hughes *et al.*, pl. 8, figs 90-92.

1988 *Marrolithus favus* (Salter); Morris, p. 135.

1988 *Marrolithus favus moderatus* Williams; Morris, p. 135.

1988 *Marrolithus inflatus* Williams; Morris, p. 135.

1988 *Marrolithus inflatus* var. *incipiens* Williams; Morris, p. 135.

1988 *Marrolithus inflatus* var. *maturus* Williams; Morris, p. 135.

1988 *Marrolithus inornatus* Whittard; Morris, p. 135.

1988 *Marrolithus lirellatus* MacGregor; Morris, p. 135.

1988 *Marrolithus primus* Williams; Morris, p. 135.

1988 *Marrolithus scalpriformis* Whittard; Morris, p. 135.

1995 *Marrolithus nefernofruaton* Vaněk, p, 10, pl. 2, fig. 12.

1996 *Marrolithus nefernofruaton* Vaněk; Havliček and Vaněk, p. 230, table 2, pl. 4, fig. 9.

2001 *Marrolithus favus* (Salter); Bettley *et al.*, pp. 942,943, text-figs 5, 6.

2001 *Marrolithus favus moderatus* Williams; Bettley *et al.*, text-fig. 6.

2001 *Marrolithus inflatus* Williams; Bettley *et al.*, text-fig. 6.

2001 *Marrolithus inflatus incipiens* Williams; Bettley *et al.*, text-fig. 6.

2001 *Marrolithus inflatus maturus* Williams; Bettley *et al.*, text-fig. 6.

Syntypes. Three fragments of cephala and lower lamellae; BGS GSM 24588-24590. Mydrim Limestone, lower Caradoc Series, Aurelucian Stage, Costonian Substage, upper *gracilis* Biozone from the road cutting between Stonyford and Pant-y-Gorphyws (SN 12061613), 1.6km north of Narberth, Pembrokeshire.

Material. Around 250 internal and external moulds of cranidia, cephala, lower lamellae, some pygidia and nearly complete trilobites. All show deformation due to both sediment compaction and tectonism. Width across cephalon ranges from 5-20mm. Limestones from South Wales have yielded well preserved silicified material. 20 partial cephala and lower lamellae of internal and external moulds from Morocco.

Distribution. Upper Llandeilo Flags, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, *gracilis* Biozone, from stream section 137m northwest of Troed-y-rhiw Farm, 1.07km SSE of Ffairfâch, Llandeilo; Glandwr, Carmarthenshire, Wales. Narbeth Group, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, *gracilis* Biozone from Plenblewin, Narberth, Pembrokeshire. Upper Llanfawr Mudstone Formation, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, *gracilis* Biozone from middle quarry, Llanfawr, Llandrindod Wells. Mydrim Limestone, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage, upper *gracilis* Biozone from Pant-y-Hendre quarry, St. Clears, Carmarthenshire. Middle Hendre Shale Formation, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, lower *gracilis* Biozone from middle road section, south of Mydrim, St. Clears, Carmarthenshire. Upper Rorrington Shale Formation, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, lower *gracilis* Biozone from Meadowtown; Holywell Brook, 64m southeast of bridge, 229m W7°S Rorrington Green, Shropshire. Rorrington Shale Formation, Upper Llanvirn to Lower Caradoc series, Llandeilian to Aurelucian stages, *teretiusculus – gracilis* biozones from 330m southeast of Lower Wood Brook Rorrington, Shropshire. Spy Wood Sandstone Formation, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage, upper *gracilis* Biozone from the north bank of Spy Wood Dingle,

Chirbury; 1km NNE of Rorrington, Shropshire. Ffairfâch Group, Middle Llanvirn, Upper Abereiddian, *murchisoni* Biozone from Golden Grove Mansion; 91m south of level crossing, Ffairfâch. Lower Llandeilo Flags Formation, Upper Llanvirn Series, Llandeilian Stage, upper *teretiusculus* Biozone from quarry 91m north Ty-gwyn Farm, 805m east of Llandeilo; 18m southeast of Careg-y-foel-gam Farm, 3.22km SSE of Llangadog, Carmarthenshire. Meadowtown Formation, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Meadowtown, Shropshire. Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from 668m northwest of Plas-yn-glyn, 915m NNE of Llanrhaiadr-ym-Mochnant; 91m NNE of Llwyn-Onn, 4.8 km west of Llanrhaiadr-ym-Mochnant; 73m north and 183m northwest of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys. Middle Rorrington Shale Formation, Lower Caradoc Series, Lower Aurelucian Stage, Lower Velfreyan Substage, lower *gracilis* Biozone from Deadman's Dingle, 30m up stream from junction with Spy Wood Brook, Shropshire. Middle Llandeilo Flags, Lower Caradoc Series, Lower Aurelucian Stage, Lower Velfreyan Substage, mid *gracilis* Biozone from 400m NNE of Dynevor Castle, Llandeilo, Carmarthenshire. Upper Andouille Formation, within a 4m band of limestone, Upper Llanvirn-basal Caradoc, Llandeilian to lowest Aurelucian, Bois de la Touche, Andouille, Laval, Brittany, France. Upper Dobrotivà Formation, Upper Llanvirn-basal Caradoc, Llandeilian to lowest Aurelucian, *Cryptograptus tricornis* Biozone, Praha-Smichov, road tunnel at Mrazovka. Izgourin Formation, First Bani Group, Caradoc Series, Aurelucian Stage, Morocco.

Diagnosis. Subquadrate fringe. Some degree of fringe inflation laterally including I_1 and I_2 arc pits, pits increase in diameter to lateral position before decreasing in size towards the posterior margin. Girder prominent frontally tapering sharply abaxially.

Recorded pit counts: E_1, 22-28 (mean, 25; I_n, 12-19 (15.5), I_n cut-off by arc I_3-I_5 (4.5); I_1, 19-29 (23.5); I_2, 16-28 (21), starting row for I_2 R, 2-5 (3); I_3, 7-23 (17), I_3 arc starts at R, 3-14 (6.5); I_4, 5-16 (11.5), I_4 starts at R, 8-13 (10); I_5, 3-10 (5) starting at R, 7-11 (15).

Remarks. Compressional deformation during burial, largely in silt and mud deposits, tectonism and whether one or both lamellae are present, has affected the extent of the fringe inflation in most material. As a result, there is considerable variation within any population sample in the number of pits involved and elevation of the inflation and so this is not always a

useful diagnostic character (see Pl. 1, Figs 3 and 4 and Section 2.2.4). All other "species" synonymised here into *M. f. favus* have been based on deformed individuals. Text-fig 4.1 shows the range and mean values of fringe pit data in the type and topotype material of the supposed species, hence the low number of specimens involved. The ranges show considerable overlap. Text-fig 4.2 shows the fringe pit data for all of the specimens ascribed herein to *Marrolithus favus favus*.

Marrolithus favus is here revised to incorporate several supposed "species" and is best viewed as an array of highly variable populations which differ in their range of variation both spatially and temporally but with considerable overlap in fringe pit numbers (see Text-Fig. 4.1). The cladistic analysis of the genus (Text-Fig. 3.27) supports the synonymy of *Marrolithus favus moderatus*, *M. inflatus*, *M. inflatus incipiens*, *M. inflatus maturus*, *M. primus*, *M. inornatus*, *M. scalpriformis* and *M. lirellatus* with *Marrolithus favus*. Some comments on them are appropriate:

Addison (unpublished PhD thesis 1974) favoured the synonymy of the subspecies *Marrolithus favus moderatus* within *M. favus favus*. This was not followed by Wilcox & Lockley (1981) nor Bettley *et al.* (2001) (also Bettley 1998 unpublished PhD thesis). Wilcox & Lockley stated that *M. favus moderatus* could be distinguished by the less angular anterolateral region on the upper lamella, a less concave lateral margin, the restriction of the swollen area to low numbers of I_1 and I_2 pits involved in the swellings on both lamellae, a lack of I_5 pits and a smaller number of E_1 pits. The first three features are highly influenced by taphonomic processes and are seen throughout the *M. favus* samples. The I_5 arc is also absent in some topotype specimens of *M. favus favus*.

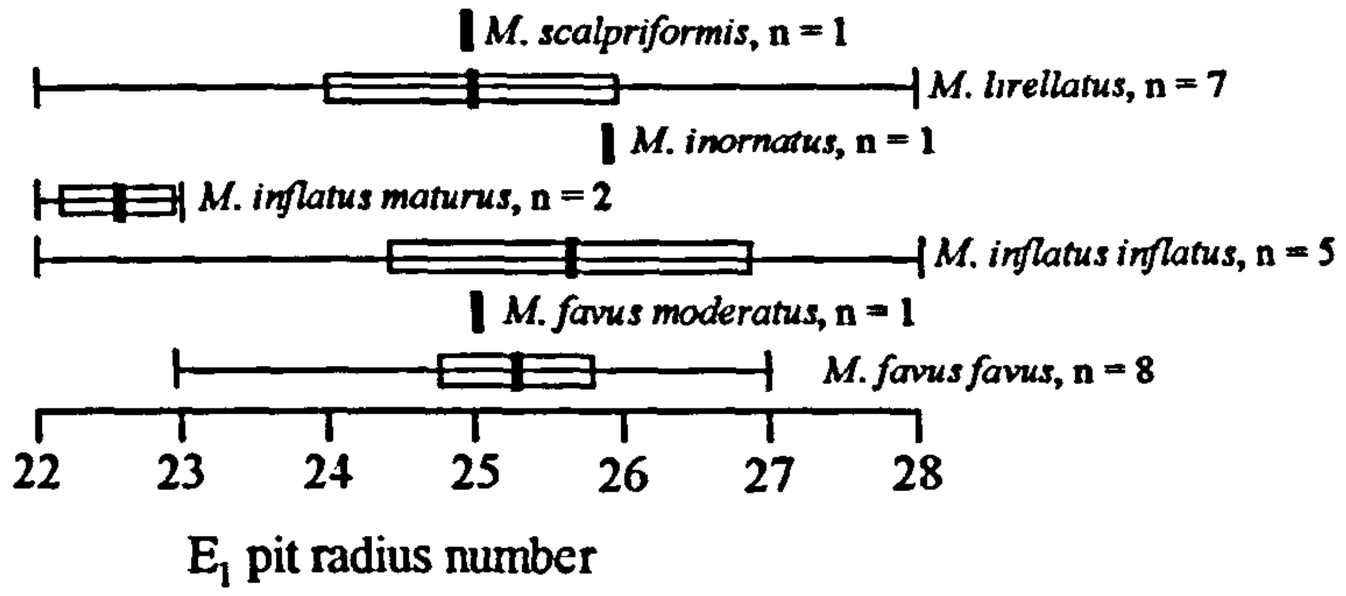
Williams (1948) established *Marrolithus inflatus* from the Lower Llandeilo Flags of Llangadog (essentially Llanvirn Series, Llandeilian Stage) as a form distinguished from *M. favus* by its gently convex cephalic outline frontally, smaller pits, absence of tubercles on the inflated area of the fringe and in the smaller area of inflation which generally affects only four pits anteriorly and never includes I_3 pits. However, tubercles are visible on the inflated area of the fringe and the shape and size of the inflations are indistinguishable from those of *M. favus*.

Williams (1948) stated that *Marrolithus inflatus maturus* from the Lower Llandeilo Flags of Llandeilo, was an "advanced" form of *M. inflatus*, with its larger area of inflated pits and

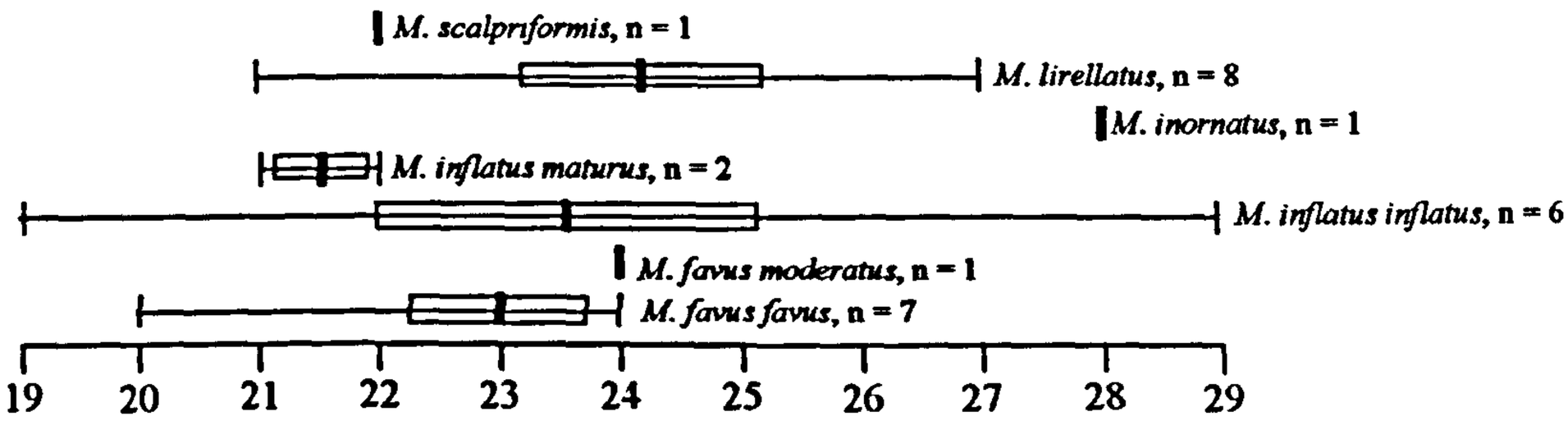
radial rows anteriorly. MacGregor (1963) distinguished *M. inflatus maturus* from the Berwyns from *M. favus* by the cephalic outline, which he stated was more strongly convex anteriorly in the former. This is here interpreted as no more than taphonomic distortion. *M. inflatus incipiens* Williams, 1948 was diagnosed by its small size. However, it is not smaller than other *Marrolithus favus*. Williams (1948) distinguished *M. inflatus incipiens* from *M. primus* by the absence of a inflated area in the holotype and paratype of the latter species. However, a peel of the holotype of *M. primus* shows a well-developed inflated area affecting arcs I_1-I_3. The fragmentary paratype cephalon preserves very little of the fringe, but does show a small area of the inflated region where a few tubercles on this area can also be observed. *M. inornatus* Whittard, 1956, was based on a flattened specimen showing a laterally extension on the cephalic margin. This feature is visible on well preserved specimens of *Marrolithus favus*.

Whittard (1958) placed the *Marrolithoides* cf. *anomalis* of Williams, 1948 in *Marrolithus* because of its inflated fringe and "distended" outline. The area ratio for this specimen has been calculated as fringe: genal lobe, 1:0.81, clearly nearer to *Marrolithus* (1:0.5) than *Marrolithoides* (1:1.23) and it therefore supports Whittard's view.

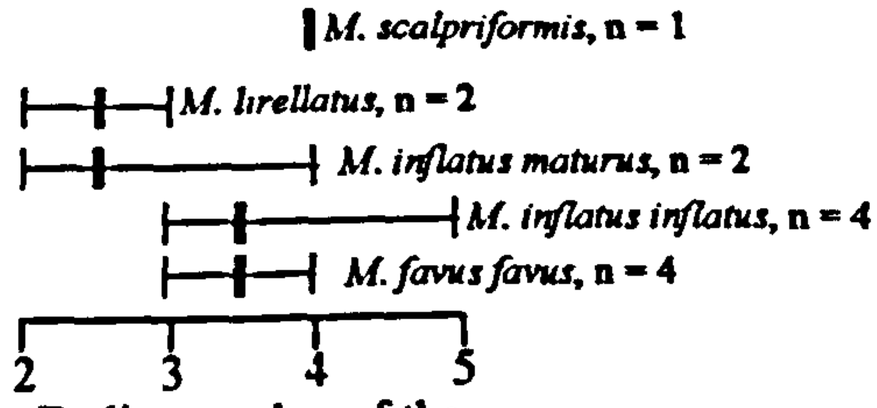
The French species *Marrolithus bureaui* was a contemporary of *M. f. favus* and shows all the features associated with the latter. It is here regarded as synonymous with *M. f. favus* (compare Pl. 1, Figs 1 and 8). The Bohemian species *Marrolithus nefernofruaton* is based on one specimen and this is here synonymised with *M. f. favus*. The Bohemian specimen and some from the Anglo-Welsh area show a lateral extension on the cephalic margin (see Section 2.2.6). This feature is also seen in some Welsh *M. arenarius* and *M. elegans*. Material from the Anti-Atlas Mountains of Morocco studied here in contains only rare specimens of *Marrolithus* from lowest Caradoc Beds. The pit counts and number of arcs are within the *M. f. favus* range of variation: E_1, 25-26 (mean, 26); I_1, 23-26 (24); I_2, 20-22 (21), starting at row 3-4; I_3 19-20, starting at row 5-6; I_4 12-14 (13), starting at row 9-10; I_n 16-18 (17), cut off by I_4-I_5. Destombes (1985) referred to undescribed *Marrolithus* from Morocco, the majority of which are herein ascribed to *Hammannaspis* gen. nov. A number of Llanvirn samples from the Anti Atlas region contains either *Marrolithus* with *Hammanaspis* or *Deanaspis* specimens. The latter do not have I_2 arc pits elevated but do have strong reticulation on holaspids as well as meraspids.



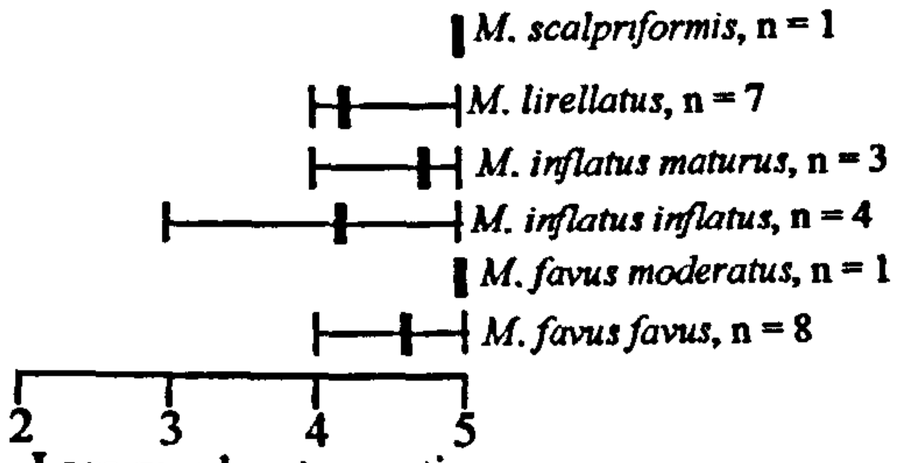
E_1 pit radius number



I_1 pit radius number

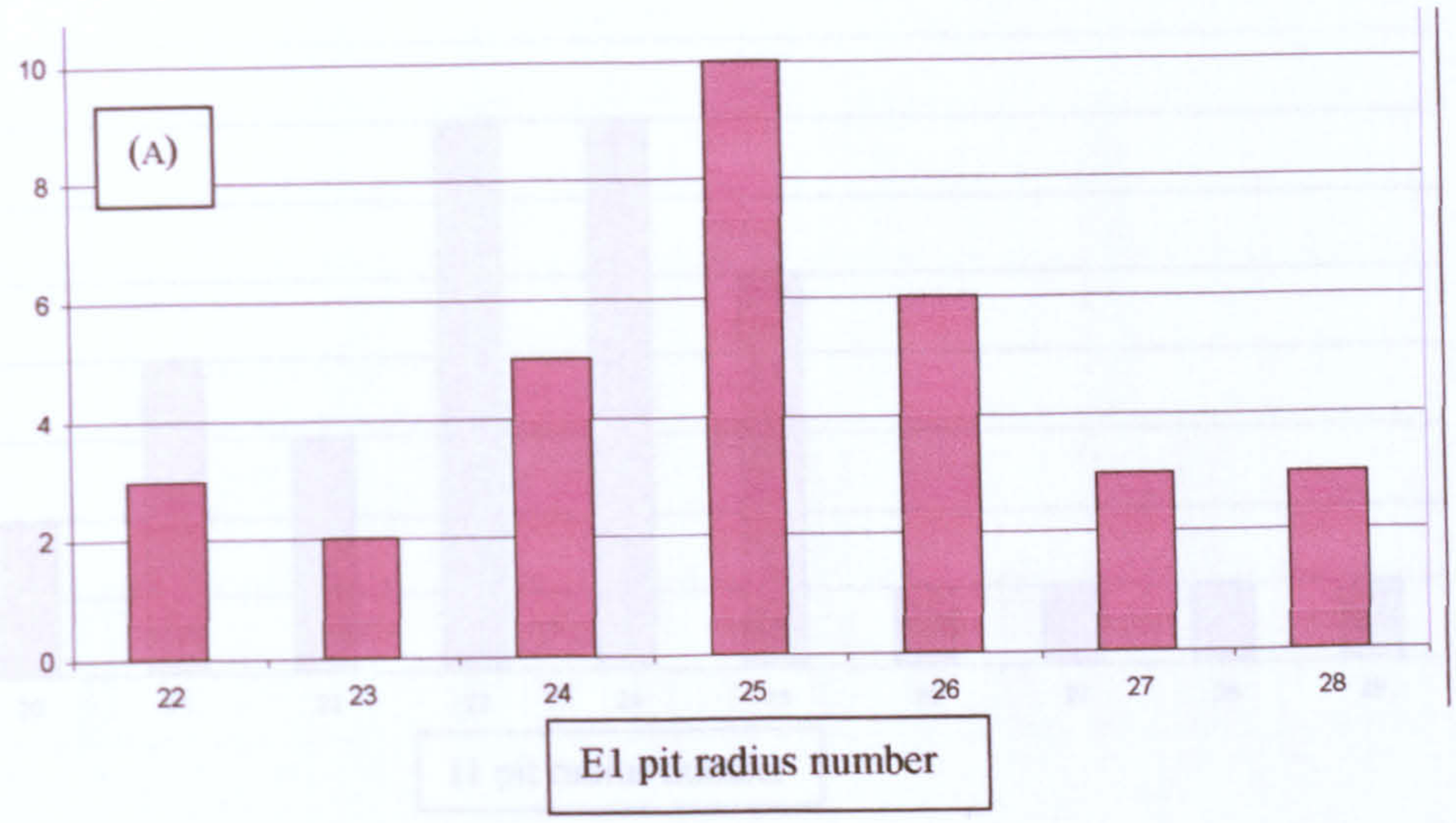


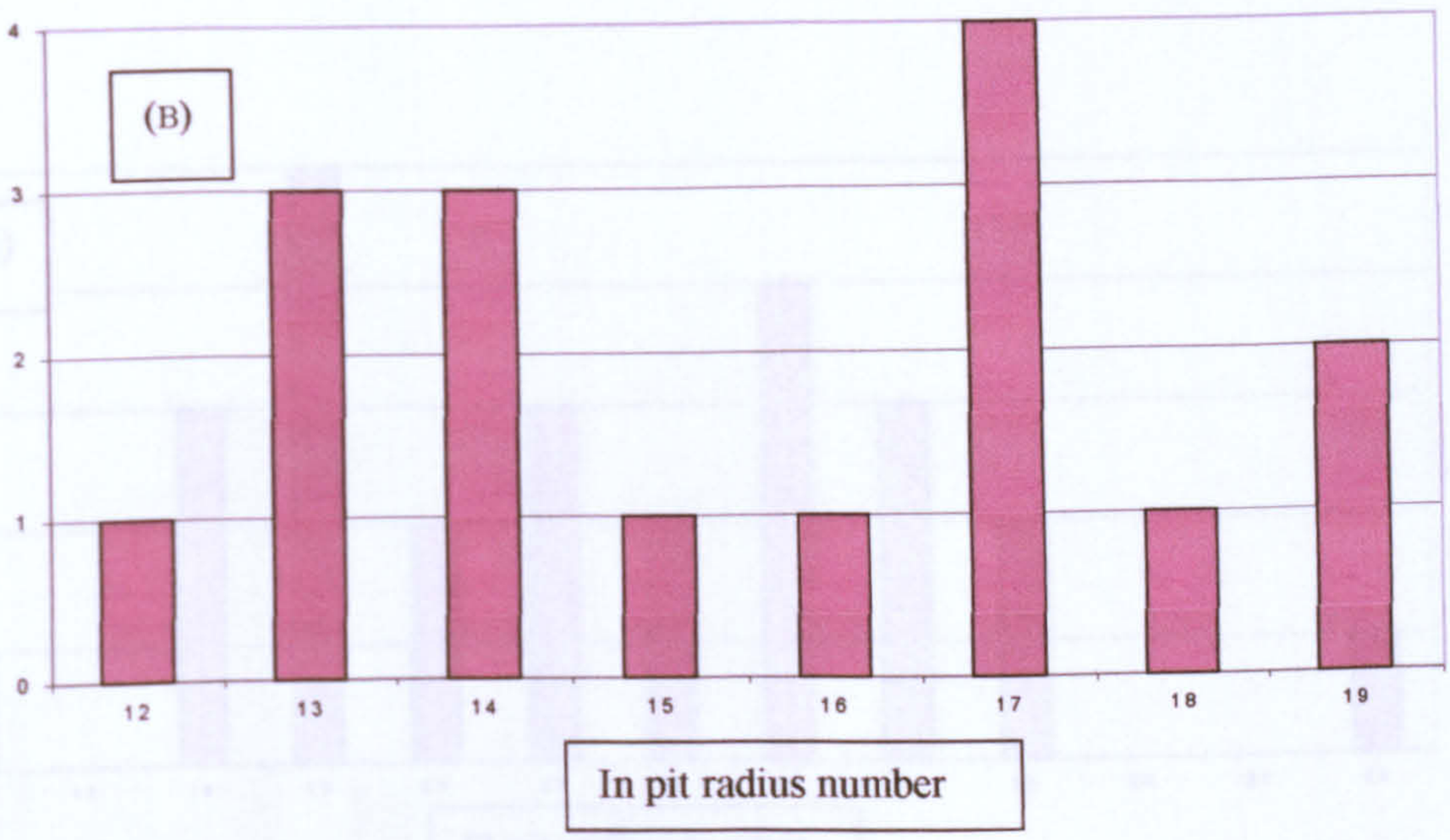
Radius number of the starting position of I_2 arc



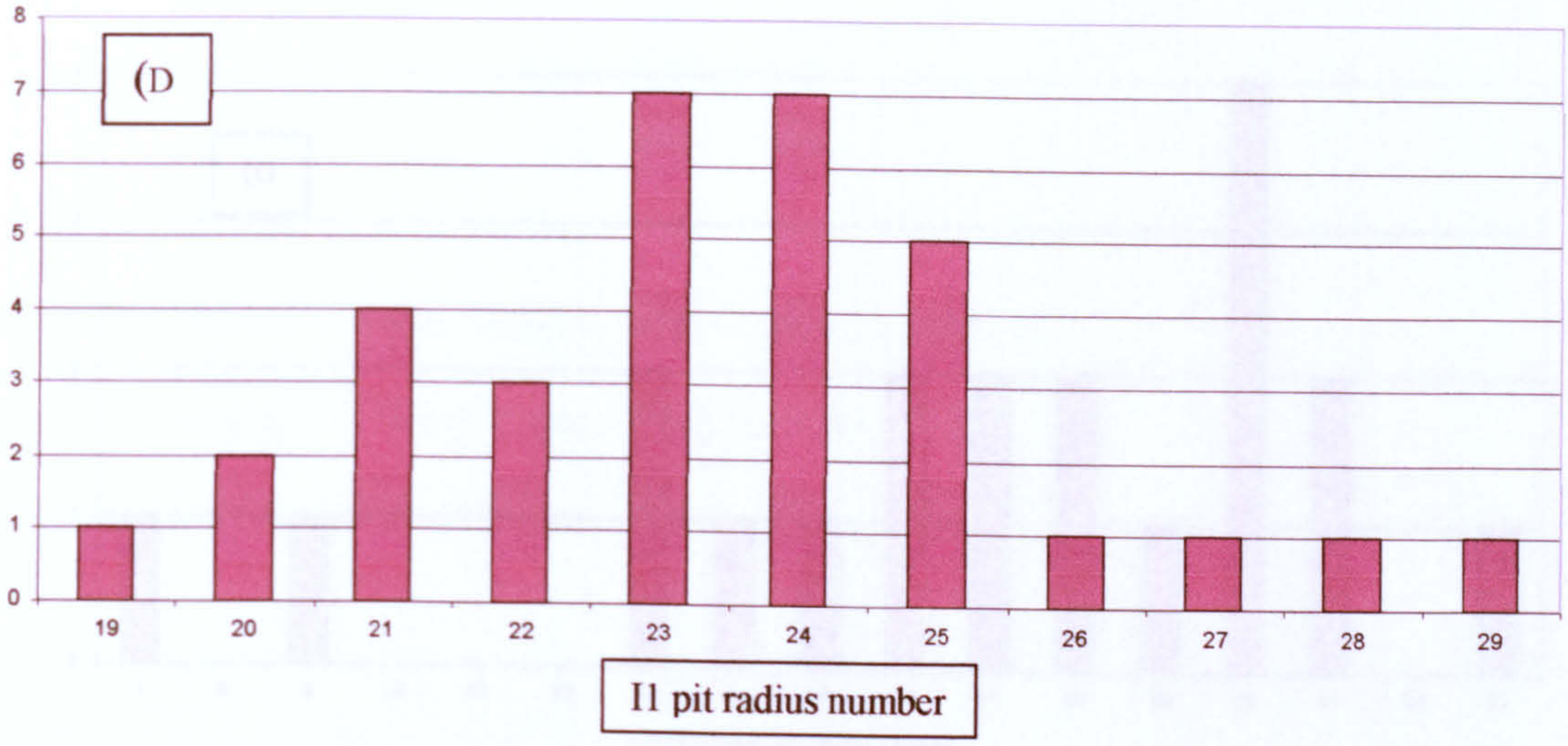
I arc number truncating I_n arc

Text-Fig. 4.1. Range and mean charts for species herein synonymised with *Marrolithus favus favus* from their respective type material.


(A)
10
8
6
4
2
0
22
23
24
25
26
27
28
E1 pit radius number


(B)
4
3
2
1
0
12
13
14
15
16
17
18
19
In pit radius number

(c)
18
16
12
10
6
4
I3
I4
I5
In arc cut off arc


(D
8
7
6
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19
20
21
22
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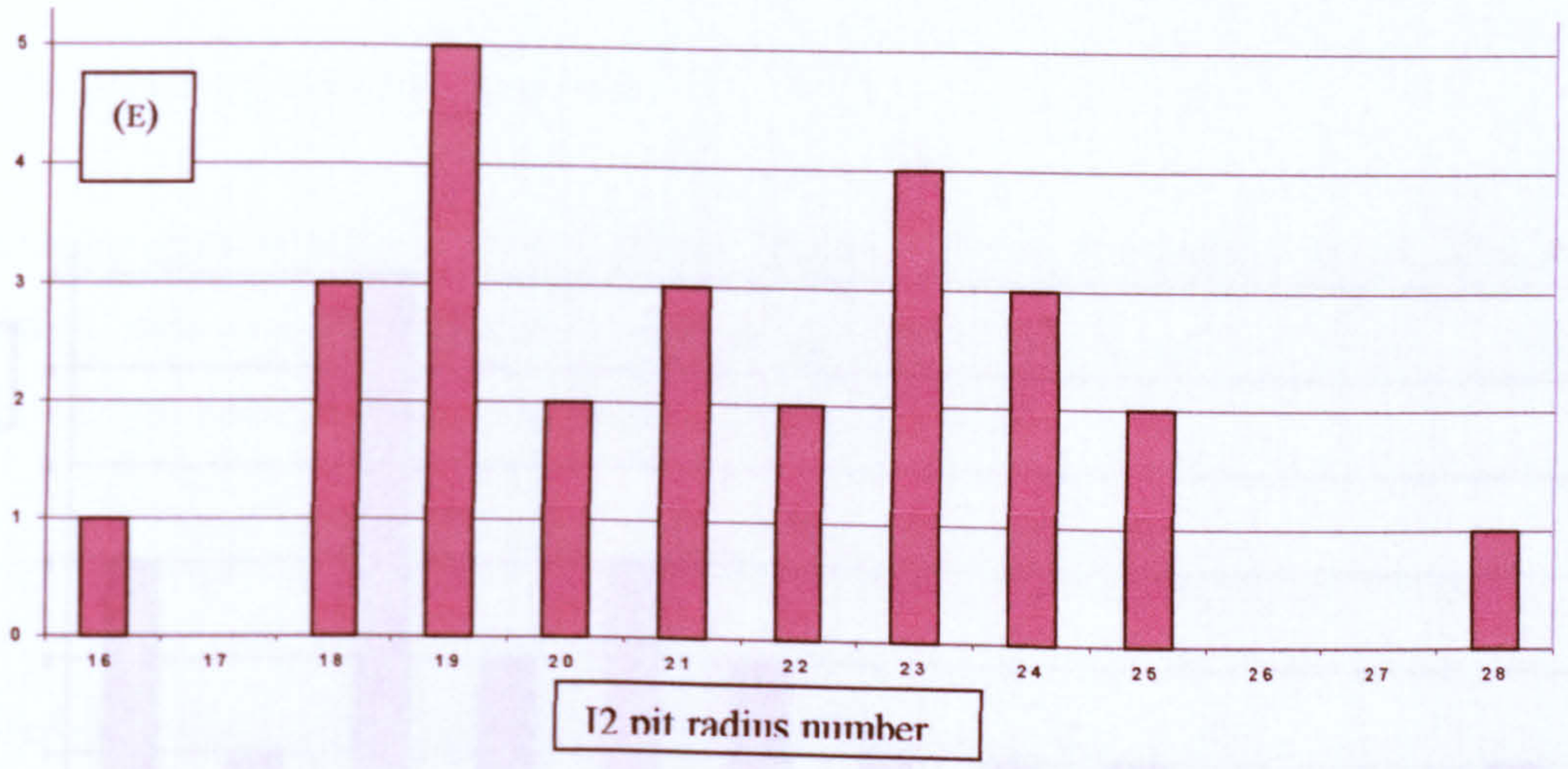
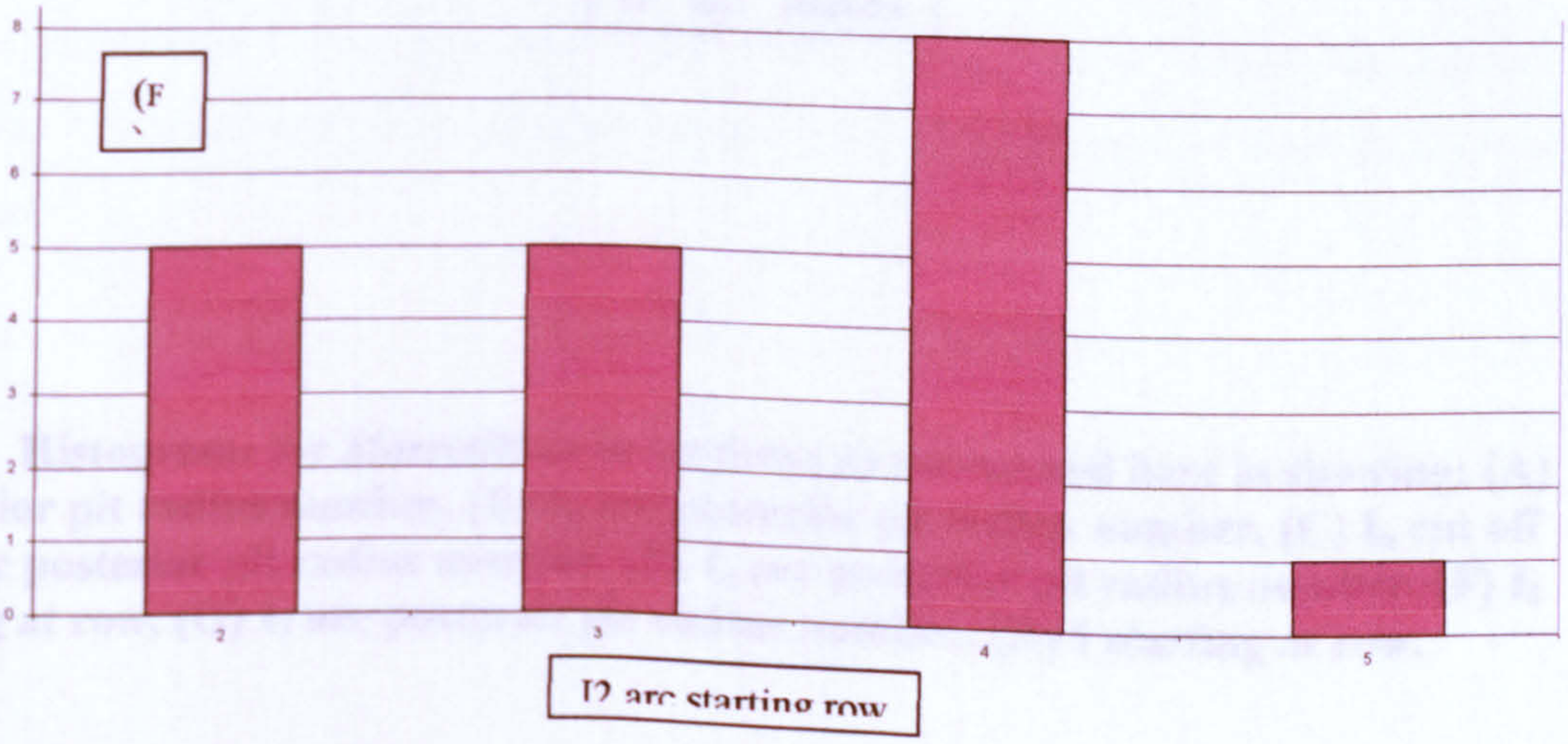
24
25
26
27
28
29
I1 pit radius number


(E)
5
4
3
2
1
0
16
17
18
19
20
21
22
23
24
25
26
27
28
I2 pit radius number


(F
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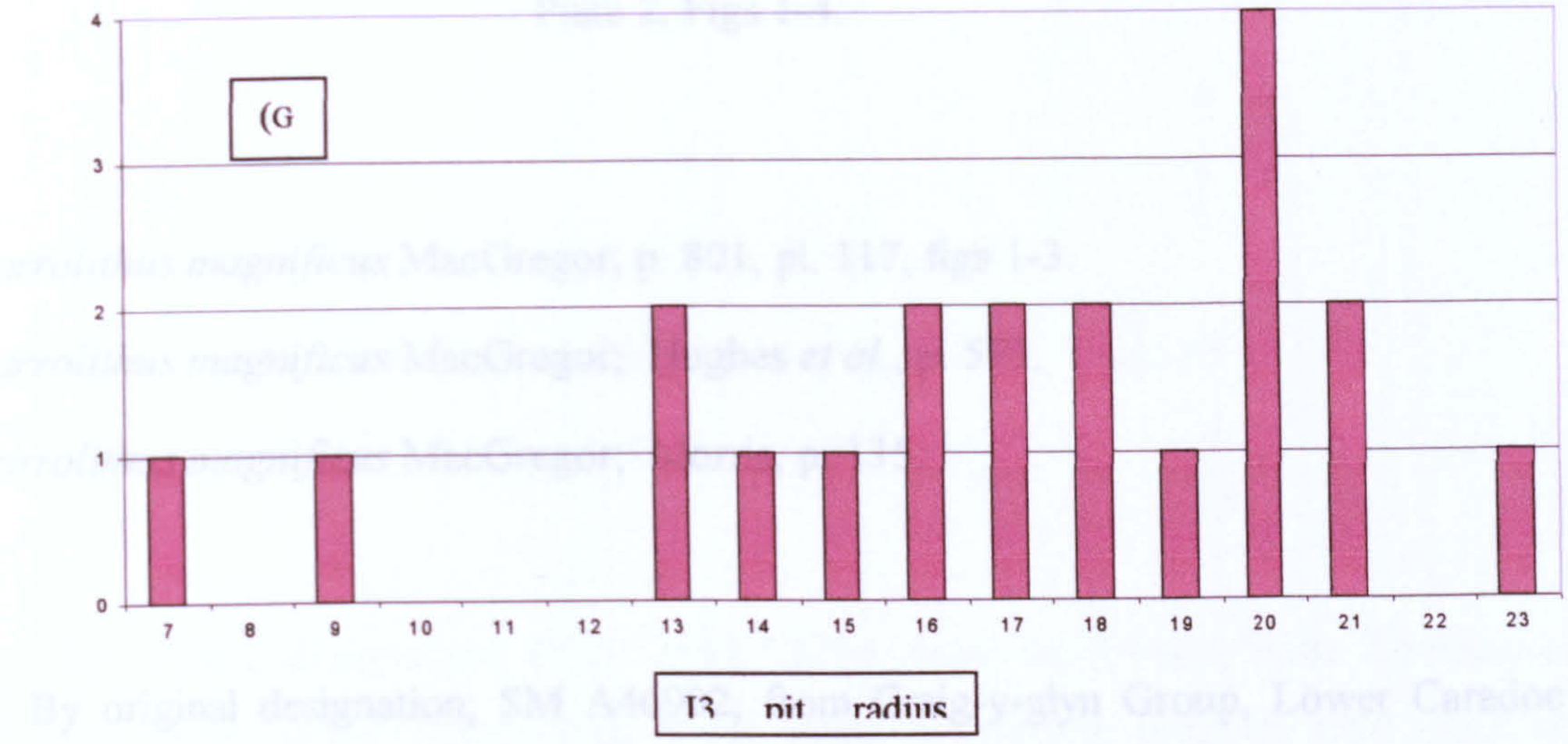
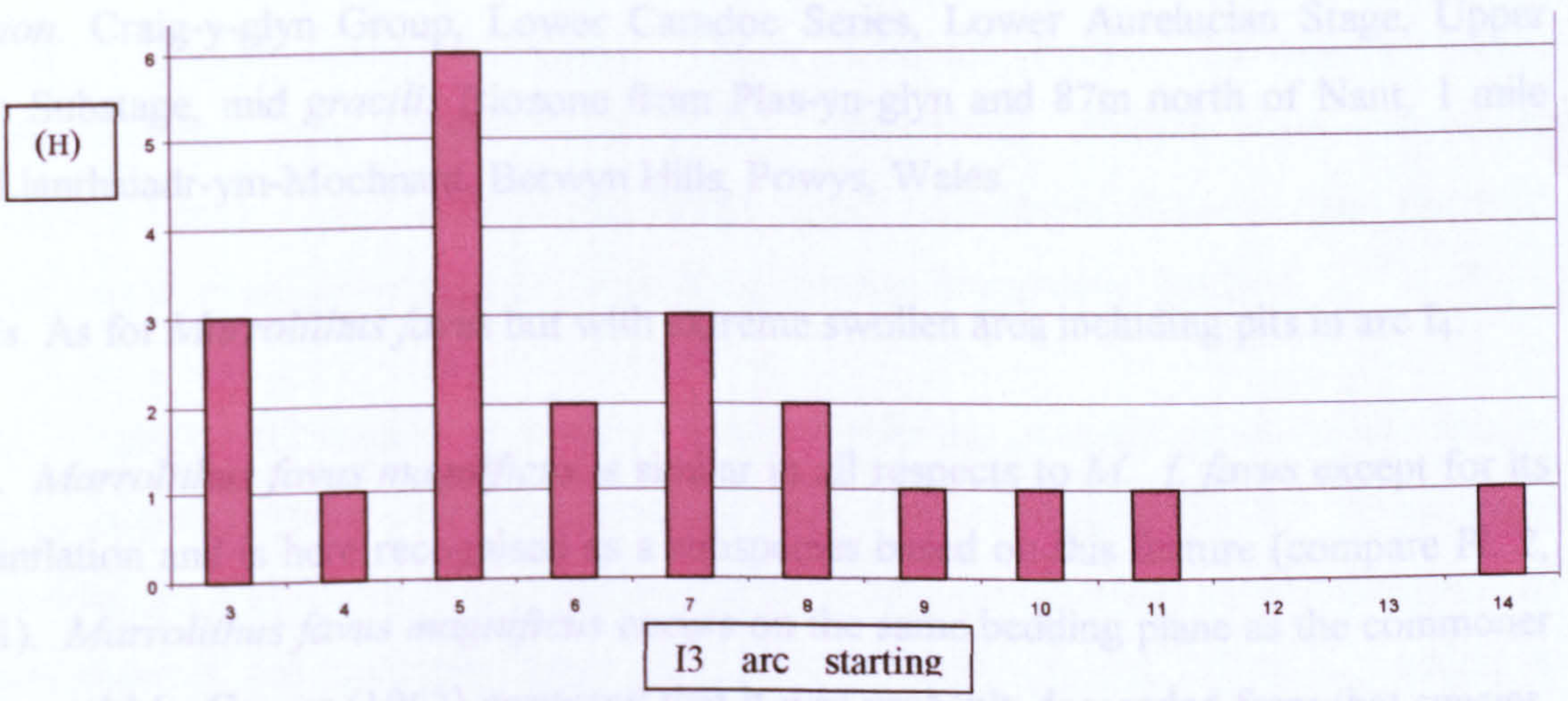
I3 arc starting row





Text-Fig. 4.2. Histograms for *Marrolithus favus favus* as recognised here in showing: (A) E_1 arc posterior pit radius number, (B) I_n arc posterior pit radius number, (C) I_n cut off arc, (D) I_1 arc posterior pit radius number, (E) I_2 arc posterior pit radius number, (F) I_2 starting at row, (G) I_3 arc posterior pit radius number, (H) I starting at row.

Marrolithus favus magnificus MacGregor, 1963

Plate 2, Figs 1-4.

1963 *Marrolithus magnificus* MacGregor; p. 801, pl. 117, figs 1-3.

1975 *Marrolithus magnificus* MacGregor; Hughes *et al.*, p. 571.

1988 *Marrolithus magnificus* MacGregor; Morris, p. 135.

Holotype. By original designation; SM A46902, from Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone of Plas-yn-glyn, Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys, Wales.

Material. 11 well preserved cephalic fragments.

Distribution. Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from Plas-yn-glyn and 87m north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys, Wales.

Diagnosis. As for *Marrolithus favus* but with extreme swollen area including pits in arc I_4.

Remarks. *Marrolithus favus magnificus* is similar in all respects to *M. f. favus* except for its extreme inflation and is here recognised as a subspecies based on this feature (compare Pl. 2, with Pl. 1). *Marrolithus favus magnificus* occurs on the same bedding plane as the commoner *M. f. favus* and MacGregor (1963) proposed that it was probably descended from that species. It is possible that it is no more than an extreme variant of *M. f. favus*. It is retained *pro tem* as a separate taxon.

Marrolithus craticulatus Whittard, 1956

Plate 3, Figs 1-4.

1956 *Marrolithus craticulatus* Whittard, p. 51, pl. 6, figs 12-16.

1975 *Marrolithus craticulatus* Whittard; Hughes *et al.* p. 570, pl. 7, fig. 89.

1988 *Marrolithus craticulatus* Whittard; Morris, p. 134, 135.

Holotype. By original designation; BGS GSM 92990, from the Betton Shale Formation, Lower Llanvirn Series, Upper Abereiddian Stage, upper *murchisoni* Biozone, field south of the lane from Meadowtown to Castle Ring, Shelve, Shropshire, England.

Material. Around 70 partial cranidia, cephala and lower lamellae generally all well preserved cephala ranging in width from 9- 20mm.

Distribution. Meadowtown Formation, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Meadowtown Quarry, Shropshire. Betton Shale Formation, Lower Llanvirn Series, Upper Abereiddian Stage, upper *murchisoni* Biozone from the field south of the lane from Meadowtown to Castle Ring, Shelve, Shropshire, England.

Diagnosis. Cephalon sub-angular in outline. Clavate glabella, does not protrude into fringe, two pairs of lateral furrows, prominent occipital ring, slender occipital spine. Genal lobes slightly swollen. E_1 and I_1 pits larger than inner pits; I_2 increases in width to lateral region. I_2 not present mesially but generally starts around row three. I_n cut off by I_5, which is overlapped posteriorly by I_4, which is in turn overlapped by I_3. There are about 15 F pits close to the genal lobe which extend just forward of the I_n cut off. Girder list and internal lists are distinct, especially laterally. Slight inflation of fringe laterally incorporating E_1, I_1 and I_2 arcs. Lower lamella shows distinct girder over entire fringe; development of first internal pseudogirder frontally. E_1, I_1 and I_2 pits considerably larger, particularly laterally, than inner pits.

Remarks. Marrolithus craticulatus is easily distinguished from *M. f. favus* by the large size of the pits in arcs I_1, I_2 and especially E_1 compared to those in the remaining arcs. It is probably ancestral to *M. f. favus*.

Marrolithus (sensu lato) *ultimus* Bancroft, 1949

Plate 3, Figs 5-8; Text-Fig. 4.3.

1941 *Marrolithus sp.* Whittington; pl. 6, fig. 20.

1949 *Marrolithus ultimus* Bancroft, p. 297, pl. 9, fig. 7.

1956 *Costonia ultima* (Bancroft); Whittard, p. 50.

1958 *Costonia ultima* (Bancroft); Dean, p. 107, pl. 26, figs 1,2.

1960 *Costonia ultima* (Bancroft); Dean, p. 87, pl. 12, figs 1-12.

1966 *Costonia ultima* (Bancroft); Whittard, p. 281, pl. 49, figs 5-8.

1975 *Costonia ultima* (Bancroft); Hughes *et al.*, p. 571, 597, pl. 8, figs 93, 94; fig. 120.

1988 *Costonia ultima* (Bancroft); Morris, p. 56.

2001 *Costonia ultima* (Bancroft); Bettley *et al.*, p. 944.

Holotype. Partial internal mould of cephalon. By original designation; BNHM In 43489, from the Hoar Edge Formation (Coston Beds-*Costonia ultima* Beds), Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone, old quarry 1.6 km ESE of Clunbury Church, 458 m west of Coston Hall, Shelve, Shropshire, England.

Material. Around 100 generally poorly preserved cephala and rare lower lamellae from Shropshire. Previous confusion over identification has led to some museum specimens from north of Cardington Hill, Shropshire, being incorrectly labelled as *C. elegans*.

Distribution. Hoar Edge Formation (Coston Beds), Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone [= *Costonia ultima* beds] from quarry 1.6 km ESE of Clunbury Church, 458 m west of Coston Hall; of Coed Brook, Hagley; old quarry 155 m south of Coston Farmhouse, Shropshire; Hoar Edge Formation, Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone from Gutter section, Bull Hill, Evenwood, Shropshire. Topmost Spy Wood Sandstone Formation, Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone from 1 km NNE of Rorrington, Shelve area, Shropshire.

Diagnosis. Subquadrate cephalic outline. E_2 frontally in a few specimens; no I_2 mesially; I_n terminated by I_4, which is terminated by I_3; I_1 and I_2 arc pit widths larger than other pits; I_3 pits equal in width to those of I_1 and I_2 posterolaterally in some specimens. Low fringe inflation of I_1 and I_2 pits posterolaterally. Low number of irregular and F pits posteriorly. Sharp girder frontally narrowing markedly anterolaterally. No first internal pseudogirder present.

Recorded pit counts: E2, 2-7 (mean, 4.5); E1, 22-29 (26.5); In 15-20 (17), In cut-off by either I3 or I4 arc; I1, 19-27 (25); I2, 19-23 (21), starting at R 0-5 (2); I3, 15-23 (19), starting at R, 4-10 (6.5); I4, 10-20 (15), starting at R11-13 (12).

Description. Subquadrate cephalic outline. Glabella clavate; occipital ring narrow, indistinct; occipital spine short; faint lateral furrows; glabellar node distinct. Up to 6 E_2 pits present frontally in about half the specimens available; I_2 not present mesially; In terminated by I_4, which in turn is overlapped by I_3. Small area of irregularly positioned pits posteriorly. No posterior margin extension and no genal prolongation. Arcs I_1 and I_2 very slightly raised laterally; girder list developed and first two internal lists. Lower lamella shows distinct girder frontally, narrowing markedly anterolaterally. I_1 and about six I_2 pits are elevated laterally on the lower lamella.

Remarks. Bancroft erected the species *ultimus* for *Marrolithus*-like specimens showing E_2 pits frontally. Whittard (1956) selected *ultimus* as the type species of his genus *Costonia* on account of this feature. Dean (1960) added that the E_1 pits become distended anterolaterally. The three main cladograms (Text-figs 3.4,6) show *Costonia ultima* as a sister taxon to *Marrolithus* or as part of a larger clade. The low fringe inflation and E_2 pits in at least half of

the population samples are the only features that differentiate *Costonia ultima* from *Marrolithus favus*. It is here considered that the presence of E_2 pits in only half the members of any population sample of *C. ultima* is insufficient reason to retain its separation from *Marrolithus*. In the light of the cladistic analysis *C. ultima* is returned to *Marrolithus* as "*sensu lato*" to reflect the small deviations from more typical *Marrolithus*.

The supposed geographical separation of "*Costonia elegans*" and "*C.*" *ultima* in Shropshire (see Section 6.1) has led to misidentification of some museum specimens by assumptions being made on the restriction of each species to particular localities, so adding to the confusion in the assignment of specimens to one or the other taxon. It is very clear from the cladistic analysis that "*C.*" *ultima* is not associated with "*Costonia*" *elegans* in any relatively low-level holophyletic group. "*Costonia*" *ultima* differs from *elegans* by its low fringe inflation, more ordered pit distribution posteriorly, low number of F and irregular pits posteriorly, no genal prolongation and the lower lamella showing a narrowing girder and I_1 and I_2 pits elevated. With the type species of *Costonia*, "*C.*" *ultima*, herein transferred back to *Marrolithus* the genus *Costonia* can no longer be retained for the species "*C.*" *elegans* which is also reassigned to *Marrolithus* (sensu lato), see below.

Marrolithus (sensu lato) *arenarius* (Whittard, 1956)

Plate 4, Figs 12-14.

1956 *Marrolithus arenarius* Whittard, p. 60, pl. 8, figs 5-9.

1956 *Marrolithus bilinearis* Whittard, p. 60, pl. 8, figs 5-9.

1956 *Marrolithus ventriculatus* Whittard, p. 62, pl. 7, figs 17, 18.

1988 *Marrolithus arenarius* Whittard; Morris, p. 134.

1988 *Marrolithus bilinearis* Whittard; Morris, p. 134.

1988 *Marrolithus ventriculatus* Whittard; Morris, p. 136.

2001 *Marrolithus* aff. *bilinearis* Whittard; Bettley *et al.*, text-fig. 6.

2001 *Marrolithus bilinearis* Whittard; Bettley *et al.*, p. 943-4, text-fig. 6.

2001 *Costonia arenaria* (Whittard); Bettley *et al.*, p. 943-4, text-fig. 6.

2001 *Costonia arenaria* (Whittard); Bettley *et al.*, p. 943-4, text-figs 5, 6.

Holotype. Internal mould of partial cephalon. By original designation; BGS GSM. 93017, from the Spy Wood Sandstone Formation, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage, upper *gracilis* Biozone from Coed Brook, 458m E12°N of Upper Ridge, Hagley, Shelve, England.

Material. Around 70 fragments of mainly internal moulds of near complete cranidia, cephala and about seven lower lamella fragments. Where measurable, cephala range in maximum width from 9- 20mm.

Distribution. Spy Wood Sandstone Formation, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage, upper *gracilis* Biozone from Coed Brook, 458m E12°N of Upper Ridge, Hagley; north side of Spy Wood Dingle, 850m east from Colcott Farm, Chirbury; 640m N27°W of Middleton Church, Rorrington, Shropshire, England. Meadowtown Formation, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone, 73m along road towards Rorrington from Meadowtown Quarry, Shropshire, England; Bryn Sion Sandstone Formation and very rarely in the Bryn Bank Limestone Formation, Narberth Group, Lower Caradoc Series, Aurelucian Stage, *gracilis* Biozone from Stonyford Farm road section, Narberth, Pembrokeshire, S. Wales; stream section in Cwm Llan Wood, 130m north of vicarage at Lampeter Velfrey, stream section 119m southwest of Pant-têg Farm, Lampeter Velfrey, Pembrokeshire, Wales.

Diagnosis. No I_2 arc mesially; I_1 and I_2 pits wider than other pits laterally; slight fringe inflation at I_1 and I_2 arcs anterolaterally. I_n cut off by I_4. Area of irregular pits posteriorly. Lower lamella shows I_1 arc raised lateral to posterolateral position; some I_2 pits involved; I_1 pits wider than others.

Recorded ranges: E1, 23-25 (mean, 27.5); In, 13-18 (15), In cut-off by arc I3-I5 (I4); I1, 20-26 (23.5); I2, 16-23 (20.5), starting at R2-6 (3.5); I3 14-19 (16.5), starting at R5-10 (7.5); I4, 4-9 (7), starting at R10-14 (12).

Description. Subquadrate cephalic outline. Glabella clavate; one pair of faint lateral furrows; glabellar node present; occipital ring narrow exsagittally; occipital pits distinct; short occipital spine. I_2 not present mesially. In terminated by I_4, which in turn is terminated by I_3. I_2 arc does not continue clearly to posterior margin. Area of irregularly positioned pits posteriorly leading to posterior margin extension. Girder list and first two internal lists present (particularly in the Welsh material). Lower lamella shows I_1 arc elevated and with increased diameters posterolaterally; some I_2 pits may be incorporated in elevation. The posterior slope of arc elevation is steep on lower lamella.

Remarks. Whittard (1958) established *Marrolithus arenarius* and *M. bilinearis* for specimens showing slight variation in elevation of I_1 and I_2 arcs. Bettley (unpublished Ph.D. thesis, 1998) assigned *M. arenarius* to *Costonia* on account of the anteriorly convergent lateral margins and small areas of anterolateral swellings affecting both lamellae. The cladistic analysis of all species and all characters show *Marrolithus arenarius* and *M. bilinearis* in the same clade with *Marrolithus* but the cladogram shown on Text-fig. 3.5, which excludes the inflation characters (23-34) show the two species as sister taxa to *Marrolithus*. To recognise this nodal separation from *Marrolithus* the term "*sensu lato*" is herein used. Bettley's concept of *Costonia arenaria arenaria* has been treated separately in the cladistic analyses from the earlier interpretation of *Marrolithus arenarius* as he also established *Costonia arenaria addisoni* for specimens he believed were intermediate between *C. arenaria* and *C. elegans*. The name *C. arenaria addisoni* was used by Bettley *et al.* (2001) without definition and so has no formal status (*nomen nudum*), see below. The lower lamellae of both *M. arenarius* of Whittard, *C. a. arenaria* of Bettley and *M. bilinearis* are virtually identical and the slight variation in inflation on their upper lamellae is insufficient to distinguish between them adequately. However, specimens from Wales show a greater number of irregular pits posteriorly including F pits than specimens from Shropshire. This feature may indicate geographical variation of the species *Marrolithus* (s. l.) *arenarius* and may explain their relative positions within the cladistic analysis (see Text-figs 3.4-6).

Marrolithus (sensu lato) *elegans* (Dean, 1960)

Plate 4, Figs 1-11; Text-Fig. 4.3.

1960 *Costonia elegans* Dean; p. 89, pl. 13, figs 1-6, 8, 9.

1988 *Costonia elegans* Dean; Morris, p. 56.

2001 *Costonia* aff. *elegans* (Dean); Bettley *et al.*, p. 943-4, text-fig. 6.

2001 *Costonia arenaria addisoni* (Whittard); Bettley *et al.*, text-fig. 6.

Holotype. Exoskeleton of nearly complete cephalon. By original designation; NHM In49744, from a limestone within the lower Hoar Edge Formation, *Harknessella subquadrata* Beds, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage from Round Nursery, 410m southeast of Harnage Grange, Shropshire, England.

Distribution. Hoar Edge Formation, lower Caradoc Series, upper Aurelucian Stage, Costonian Substage, Substage from Round Nursery, 410m southeast of Harnage Grange, quarry at east end of Black Dick's Coppice, Evenwood Shropshire and from the Bryn Banc Limestone Formation, lower Caradoc Series, upper Aurelucian Stage, Costonian Substage, 400 m north of Lower Court Farm, St. Clears, Carmarthenshire, SW Wales.

Diagnosis. E_2 pits present frontally in some eastern population samples; I_2 arc not continuous frontally. Six I_1 pits on lateral inflations but, no I_2. I_n cut off by I_4 arc. High number (around 20-30) of irregularly positioned pits including F pits posteriorly; slight genal prolongation and posterior extension. Lower lamella shows distinct girder around fringe and high elevation of I_1 arc only, including eight or fewer pits.

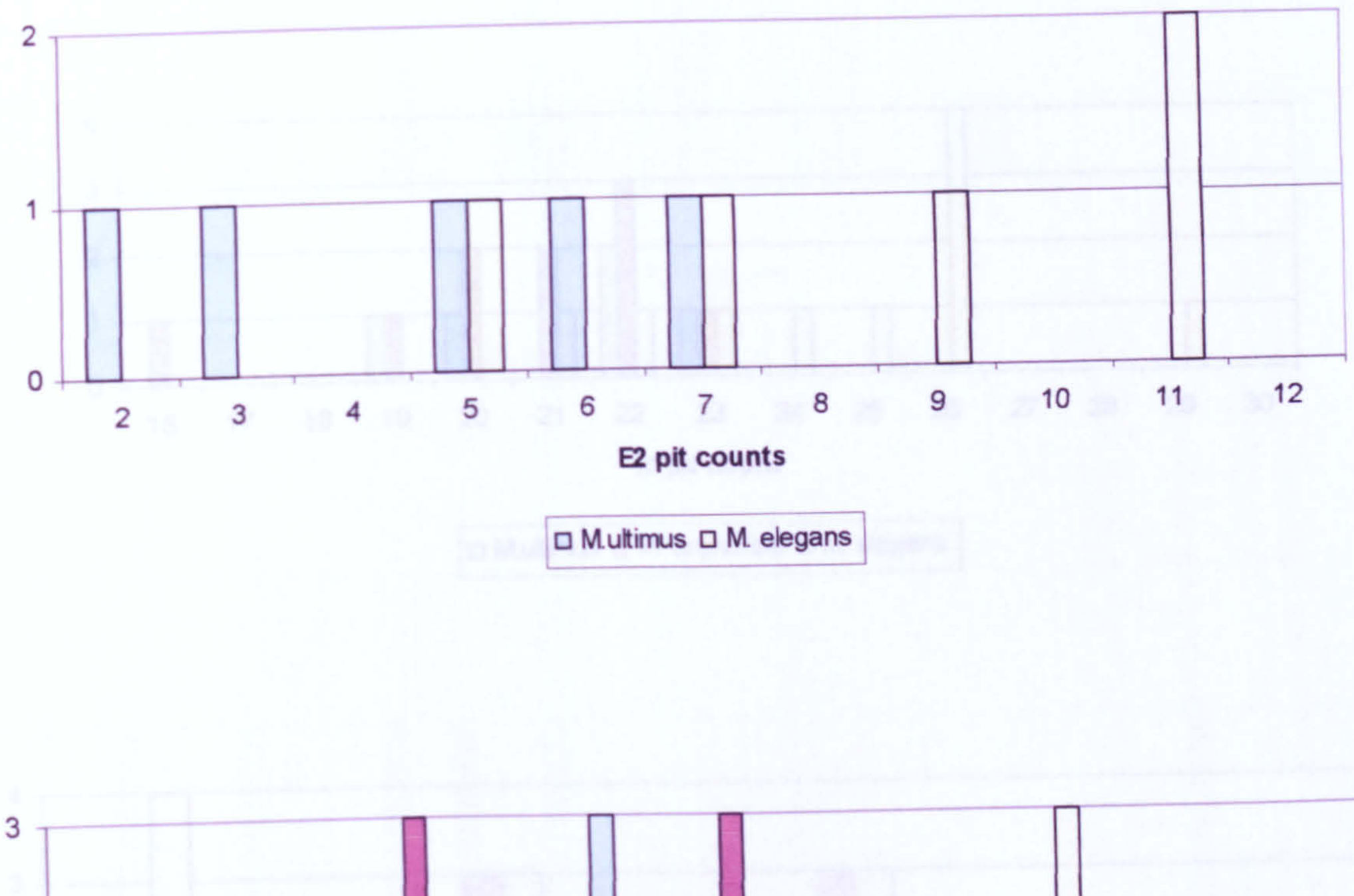
Description. Similar to *Marrolithus* (s. l.) *arenaria* except that the fringe inflations are higher and fewer pits are involved. A few pits E_2 are present frontally in some specimens in the most easterly samples (in Shropshire).

Recorded range and mean pit counts: E_2, about 5-11 (mean, 8.6) in around 60% of specimens from Shropshire E_1, 27-35 (31); I_n, 12-19 (16); I_n cut off by arc I_3-I_5 (I_4); I1, 23-30 (26); I_2, 21-29 (25), I_2 arc starts at R, 0-7 (3); I_3, 5-23 (18.5), I_3 starts at R, 3-12 (7); I_4, 4-22 (11), starting at R, 5-15 (9); I_5 6-11 (7.5), starting at R 11.

Remarks. *Marrolithus elegans* shows some degree of geographical variation. The western samples of "*Costonia arenaria addisoni*" (*nomen nudum*) of Bettley *et al.* (2001) show higher inflation of fewer pits than the Shropshire specimens "*C.*" *elegans* of Dean (1960) (see Pl. 4, Figs 1 and 3, Text-Fig 6.4). Increased numbers of F pits and randomly distributed pits posteriorly and some specimens containing E_2 pits frontally also distinguish the Shropshire specimens from the Welsh samples. This variation is reflected in the cladistic analysis with "*C.*" *elegans* and "*C.*" *arenaria addisoni* showing some degree of separation on all cladograms (see Text-figs 3.4-6).

The large number of irregular and F pits posteriorly, more localised fringe inflation on both the upper and lower differentiate *M.* (s.l.) *elegans* from *Marrolithus* (s. l.) *ultimus*. *M.* (s.l.) *elegans* generally contains higher pit counts than *M.* (s.l.) *ultimus* and *M.* (s.l.) *arenarius*. Dean (1960) stated that *elegans* marked a transition, both morphological and stratigraphical, between the genera *Marrolithus* and *Reuscholithus*. The inflated anterolateral area of the fringe is particularly characteristic of *Marrolithus*, but the outline of the cephalon and the numerous pits posteriorly are more typical of *Reuscholithus* and may indicate a possible ancestor for *Reuscholithus*.

Juvenile specimens of *M.* (s.l.) *elegans* show no fringe inflation on the upper lamella and are therefore reminiscent of *M.* (s.l.) *ultimus*. Two silicified partial cephala collected by Dr R. Addison show juveniles with the faintest of upper lamella inflation. These individuals possess prominent elevations of the girder (keels) at the lateral area on the lower lamella, see Pl.4 figs 6-11.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E2 pit counts
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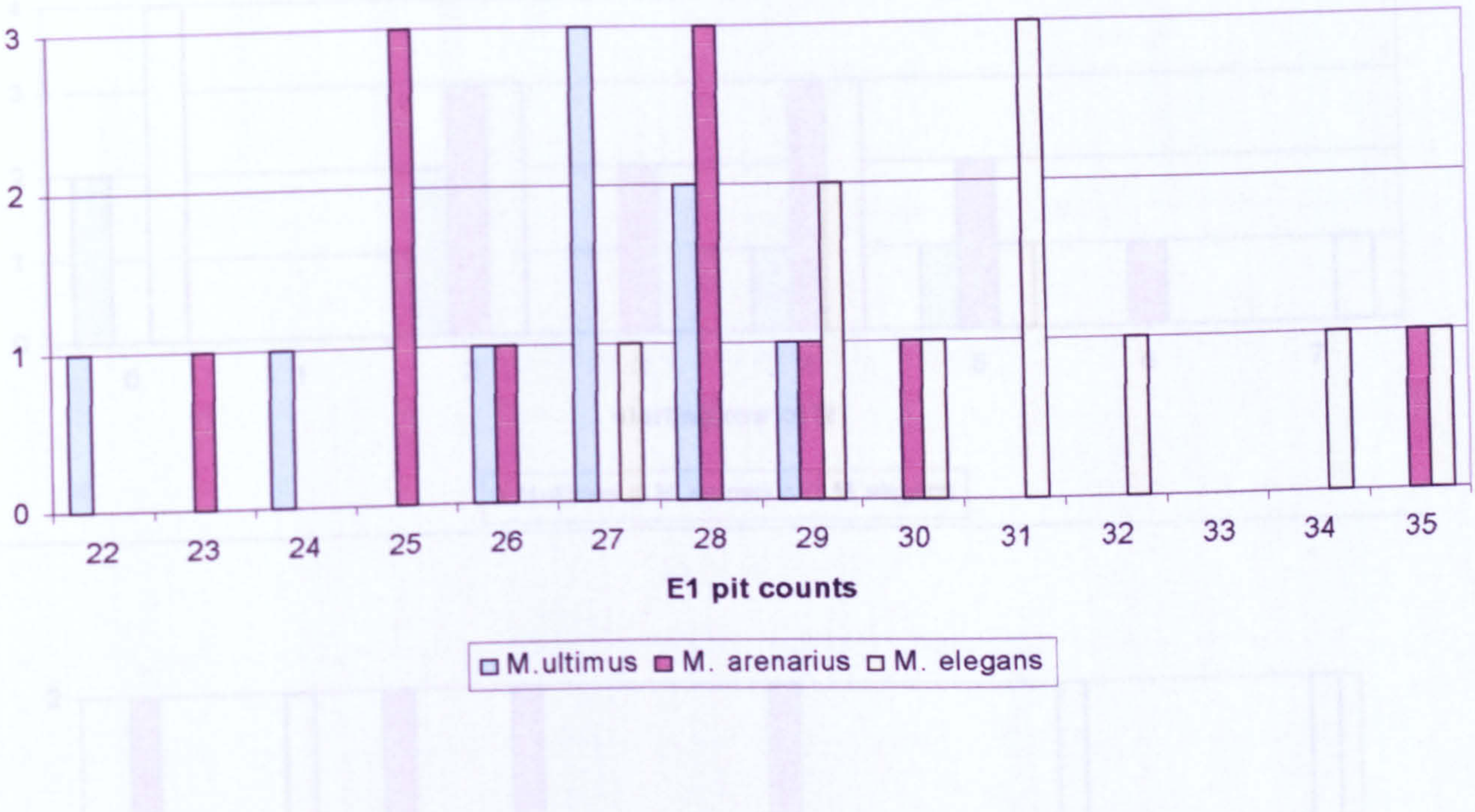
M. elegans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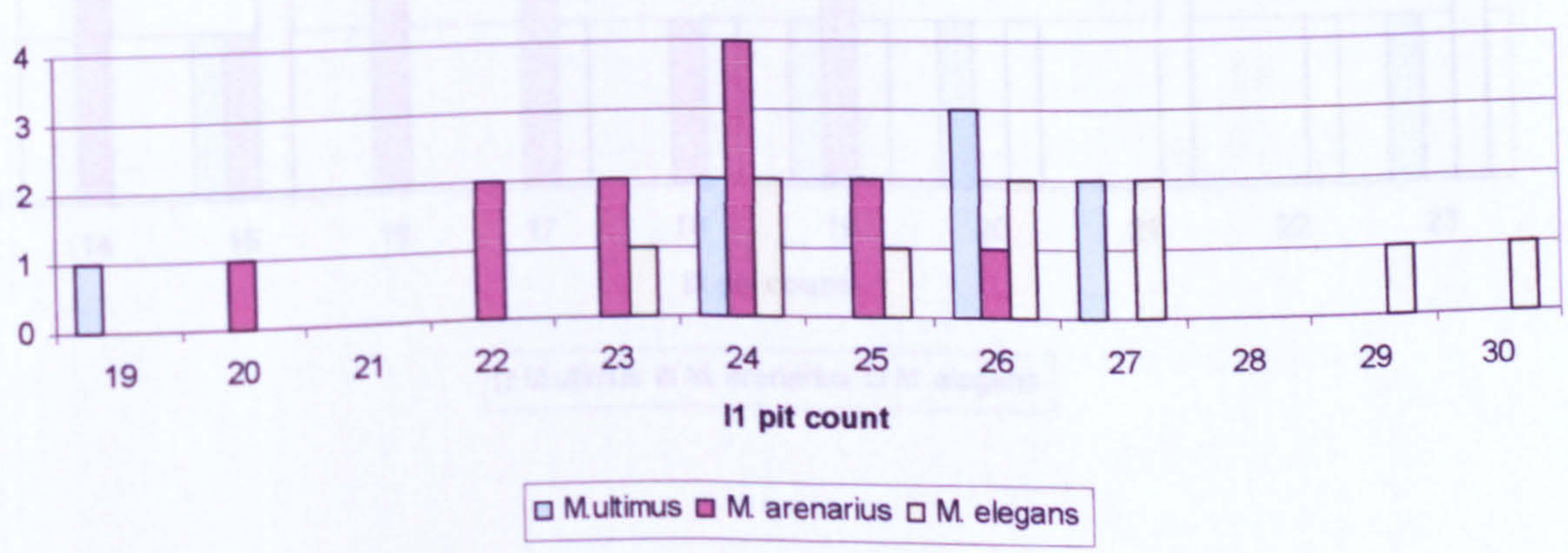
35
E1 pit counts
M.ultimus
M. arenarius
M. elegans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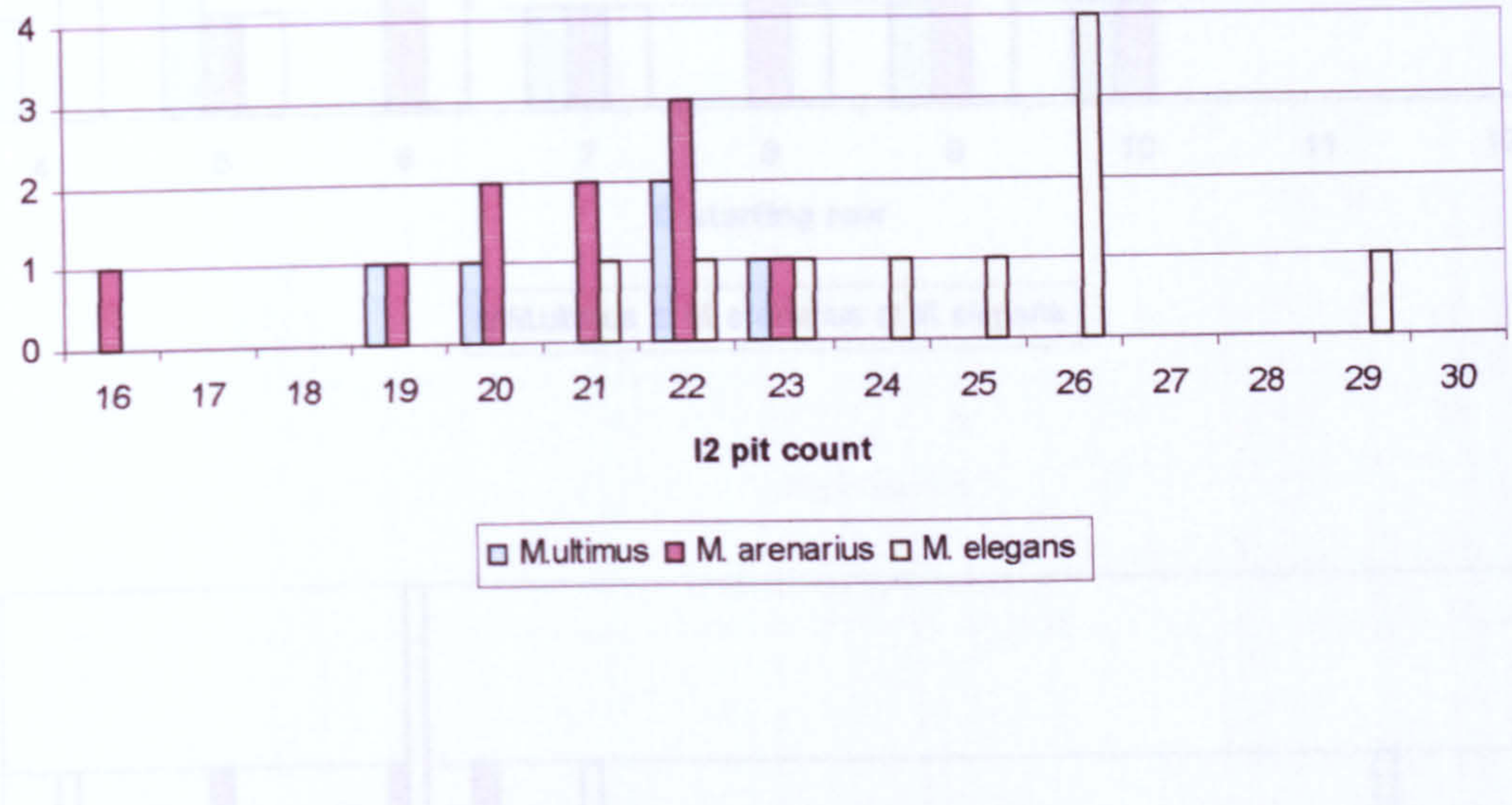
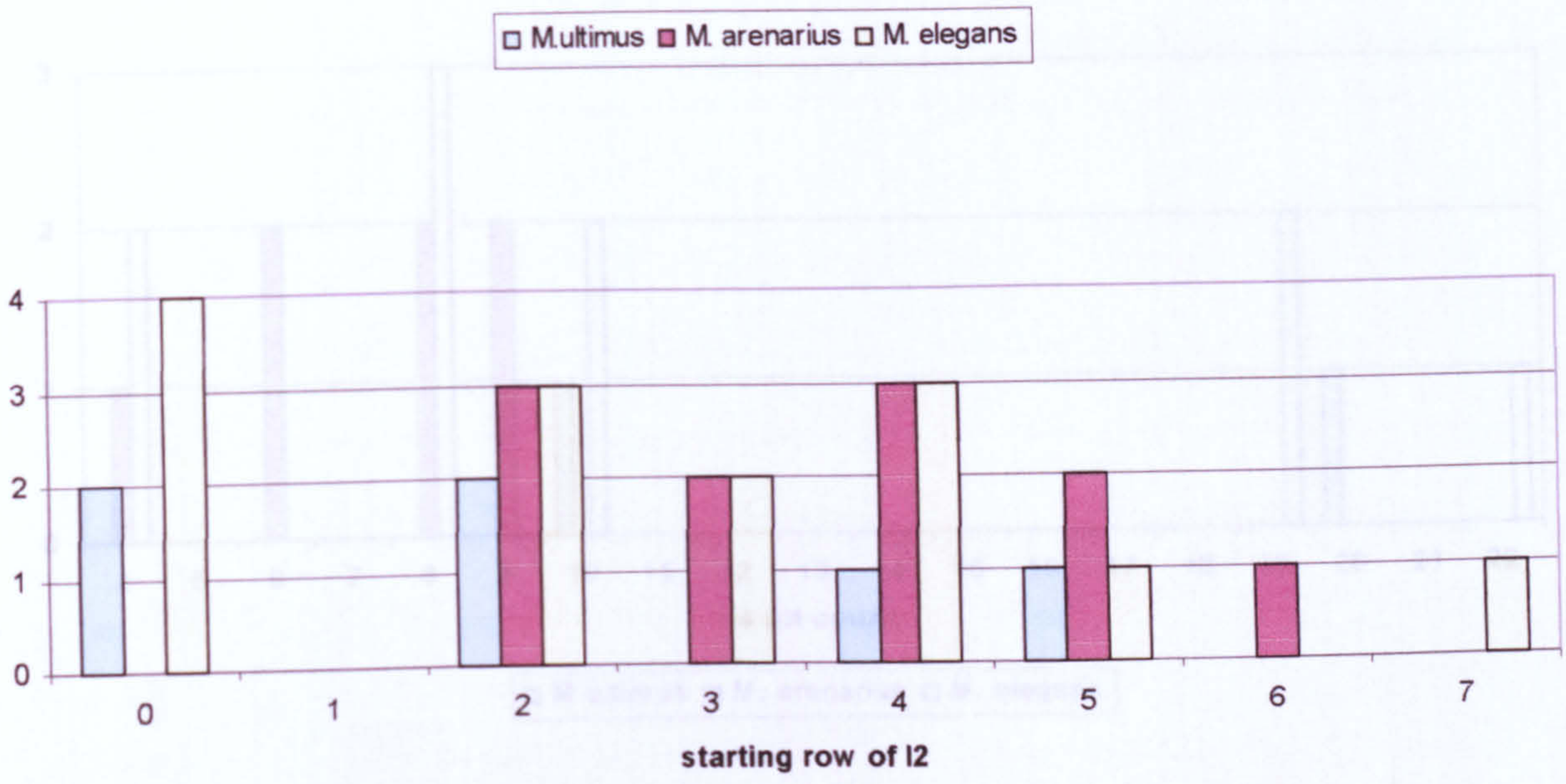
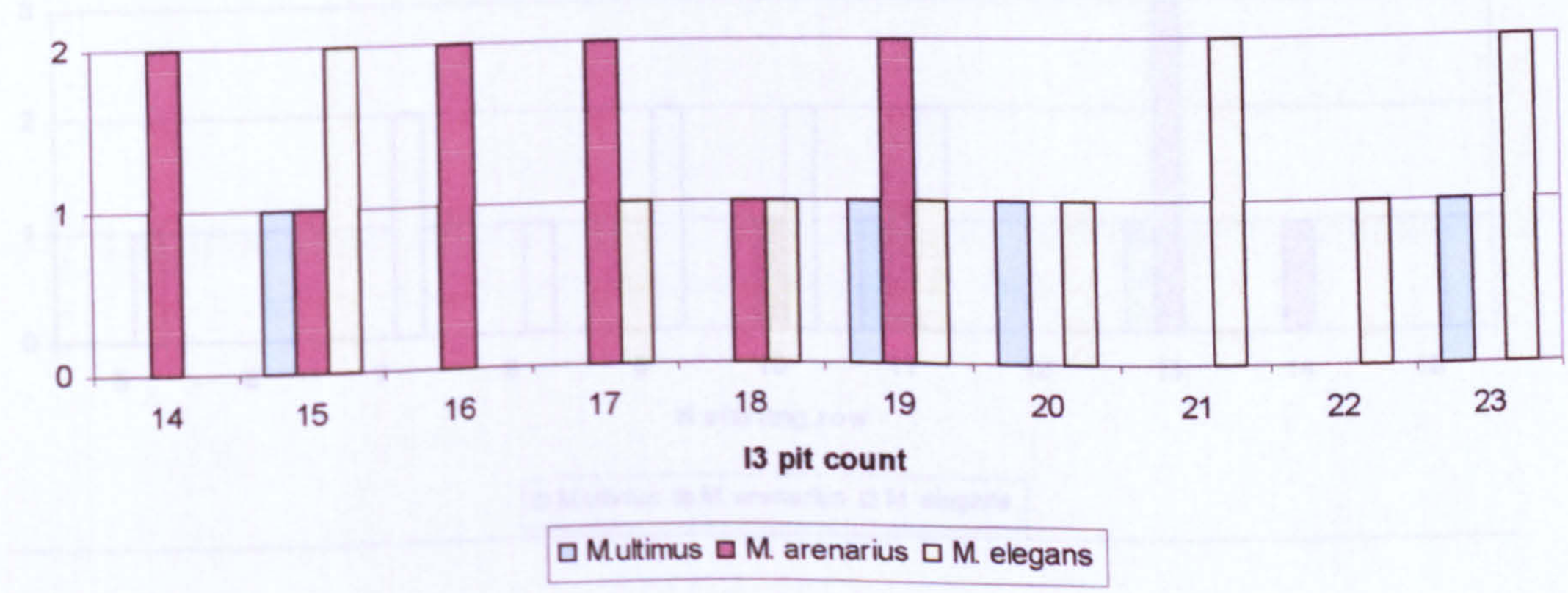
I1 pit count
M.ultimus
M. arenarius
M. elegans



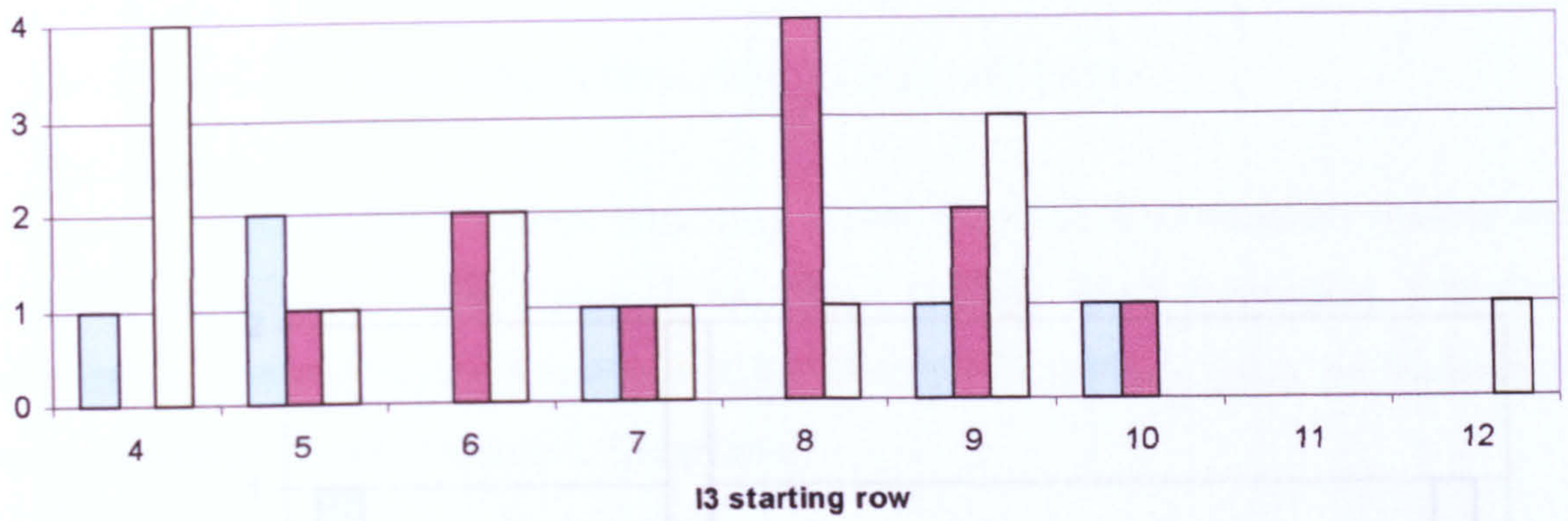
l2 pit count



starting row of l2



l3 pit count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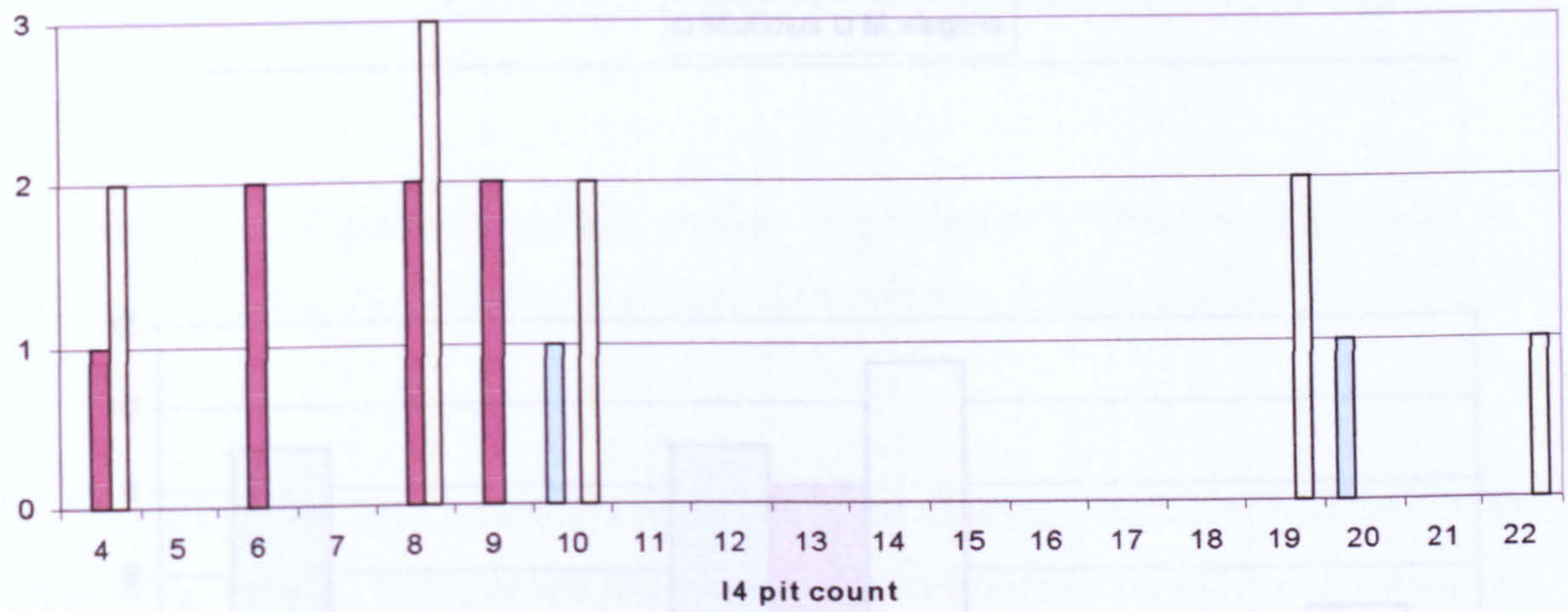
l3 starting row
M.ultimus
M. arenarius
M. elegans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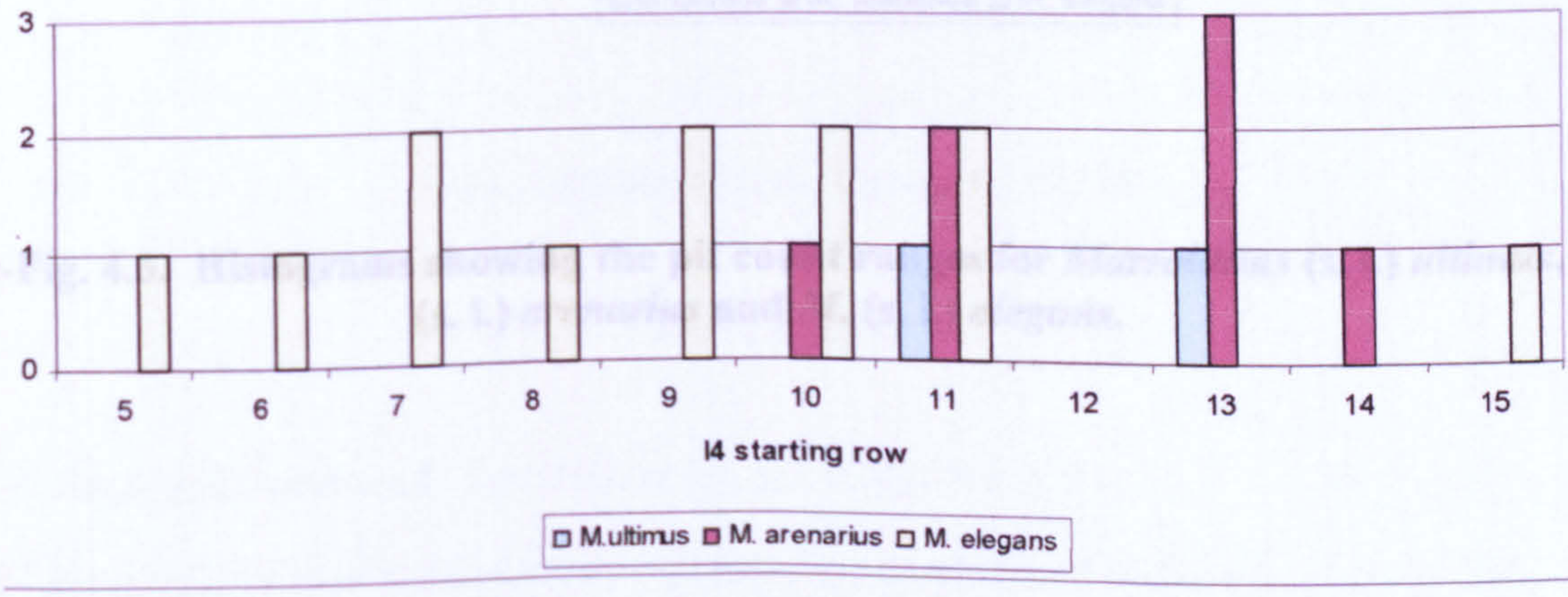
l4 pit count
M.ultimus
M. arenarius
M. elegans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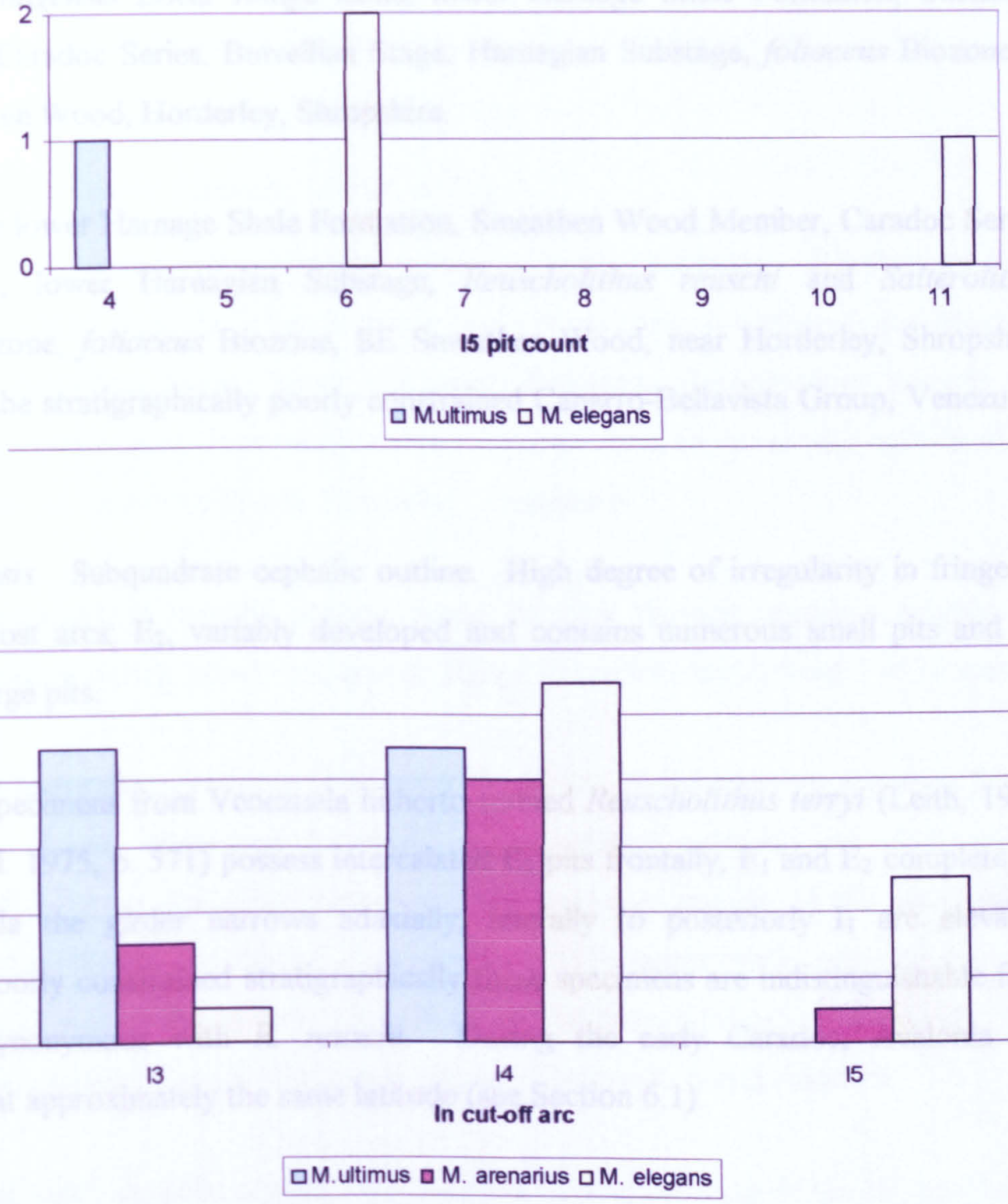
l4 starting row
M.ultimus
M. arenarius
M. elegans



Text-Fig. 4.3. Histograms showing the pit count ranges for *Marrolithus* (s. l.) *ultimus*, *M.* (s. l.) *arenarius* and *M.* (s. l.) *elegans*.

Genus **REUSCHOLITHUS** Bancroft, 1929*b*

Type species. *Reuscholithus reuschi* Bancroft, 1929*b*, from the *Reuscholithus reuschi* and *Salterolithus harnagensis* Local Range Zone; lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, Harnagian Substage, *foliaceus* Biozone of southeast Smeathen Wood, Horderley, Shropshire.

Range. From the lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, lower Harnagian Substage, *Reuscholithus reuschi* and *Salterolithus harnagensis* Biozone, *foliaceus* Biozone, SE Smeathen Wood, near Horderley, Shropshire, England. From the stratigraphically poorly constrained Caparro-Bellavista Group, Venezuela, South America.

Emended diagnosis. Subquadrate cephalic outline. High degree of irregularity in fringe pit distribution in most arcs; E_2, variably developed and contains numerous small pits and I_{1-2} have relatively large pits.

Remarks. The specimens from Venezuela hitherto termed *Reuscholithus terryi* (Leith, 1938) (see Hughes et al. 1975, p. 571) possess intercalated E_3 pits frontally, E_1 and E_2 complete, on the lower lamella the girder narrows adaxially, laterally to posteriorly I_1 arc elevated. Although very poorly constrained stratigraphically these specimens are indistinguishable from and therefore synonymous with *R. reuschi*. During the early Caradoc, Avalonia and Venezuela were at approximately the same latitude (see Section 6.1).

Reuscholithus reuschi Bancroft, 1929*b*

Plate 7, Figs1-7.

1929*b* *Reuscholithus reuschi* Bancroft, p. 82, pl. 1, figs 3-5.

1938 *Trinucleus* (*Cryptolithus*) *reuschi* (Bancroft); Stubblefield *in* Pocock *et al.*, p. 256.

1938 *Cryptolithus terryi* Leith, pp. 341-342, pl. 1, fig. 2.

1949 *Reuscholithus reuschi* Bancroft; Bancroft, p. 297, pl. 9, fig. 3.

1954 *Onnia terryi* (Leith); Whittington, pp.1-5, pl. 1, figs 1-7.

1958 *Reuscholithus reuschi* Bancroft; Dean, pl. 26, fig. 3.

1960 *Reuscholithus reuschi* Bancroft; Dean, p. 91, pl. 14, figs 1-14.

1975 *Reuscholithus reuschi* Bancroft; Hughes *et al.*, p. 571, pl. 8, figs 95, 96.

1975 *Reuscholithus terryi* (Leith); Hughes *et al.*, p. 571.

1988 *Reuscholithus reuschi* Bancroft; Morris, p. 203.

Lectotype. Part and counterpart of internal mould of partial cephalon. Selected by Dean (1960); BNHM In42080 from the lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, lower Harnagian Substage, *Reuscholithus reuschi* and *Salterolithus harnagensis* local Biozone, *foliaceus* Biozone from the trackway outside of the southeastern corner of Smeathen Wood, Horderley, Shropshire.

Material. 200 specimens of cranidia, cephala, lower lamellae, thoracic segments, pygidia and rare complete trilobites mostly poorly preserved. Range in cephalic width from 2 to 30 mm.

Distribution. The lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, lower Harnagian Substage, *Reuscholithus reuschi* and *Salterolithus harnagensis* local Biozone, *foliaceus* Biozone of the trackway outside of the southeastern corner of Smeathen Wood, Horderley; Caer Caradoc Hill; north bank, 65m below weir, Coundmoor Brook; Wyresyche quarry, Little Stretton, all from Shropshire, England. Also from the poorly constrained Caparro-Bellavista Group, Venezuela, South America.

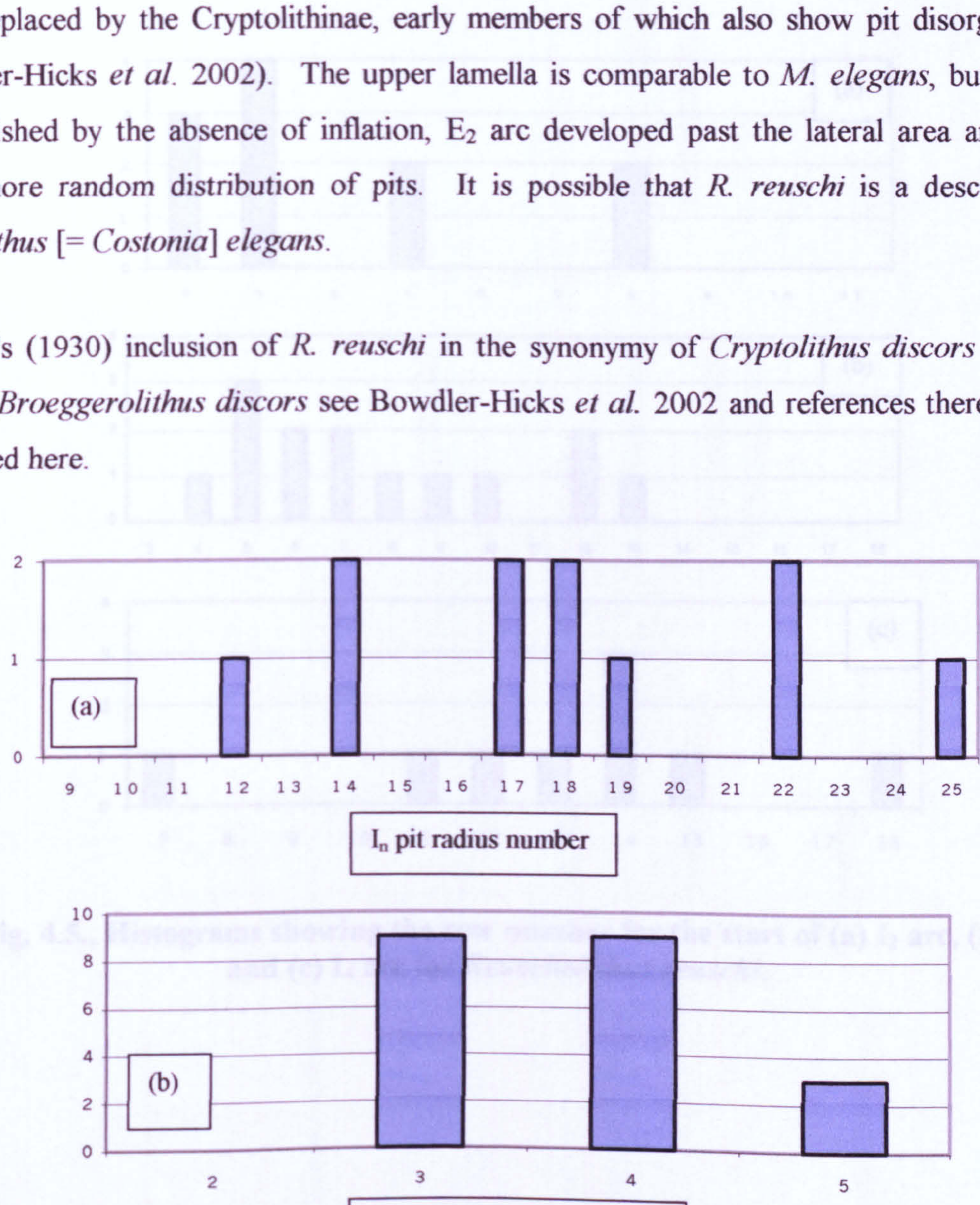
Diagnosis. Subquadrate cephalic outline. High degree of irregularity in fringe pit distribution in most arcs; E_2, variably developed and contains numerous small pits and I_{1-2} have relatively large pits. Recorded pit counts E_2, 40-45 (mean, 42); E_1, 26-38 (34); I_1, 25-26 (25.5); I_2, 18-26 (23), starting at around row 4; I_3, 18-27 (22), starting at around row 8; I_4, 9-27 (19), starting at around row 13; I_5, 15-20 (19); around 34 F pits and irregular pits.

Description. Subquadrate cephalic outline. Glabella slightly clavate. E_1, E_2, I_1 and I_n arcs complete frontally. Some specimens show a few E_3 pits frontally (usually at least partly intercalated with E_2). E_2 pits are much smaller than E_1 pits, E_1, I_1 and I_2 are wider posterolaterally compared to other arc pits. Inner arcs show some irregularity in radial

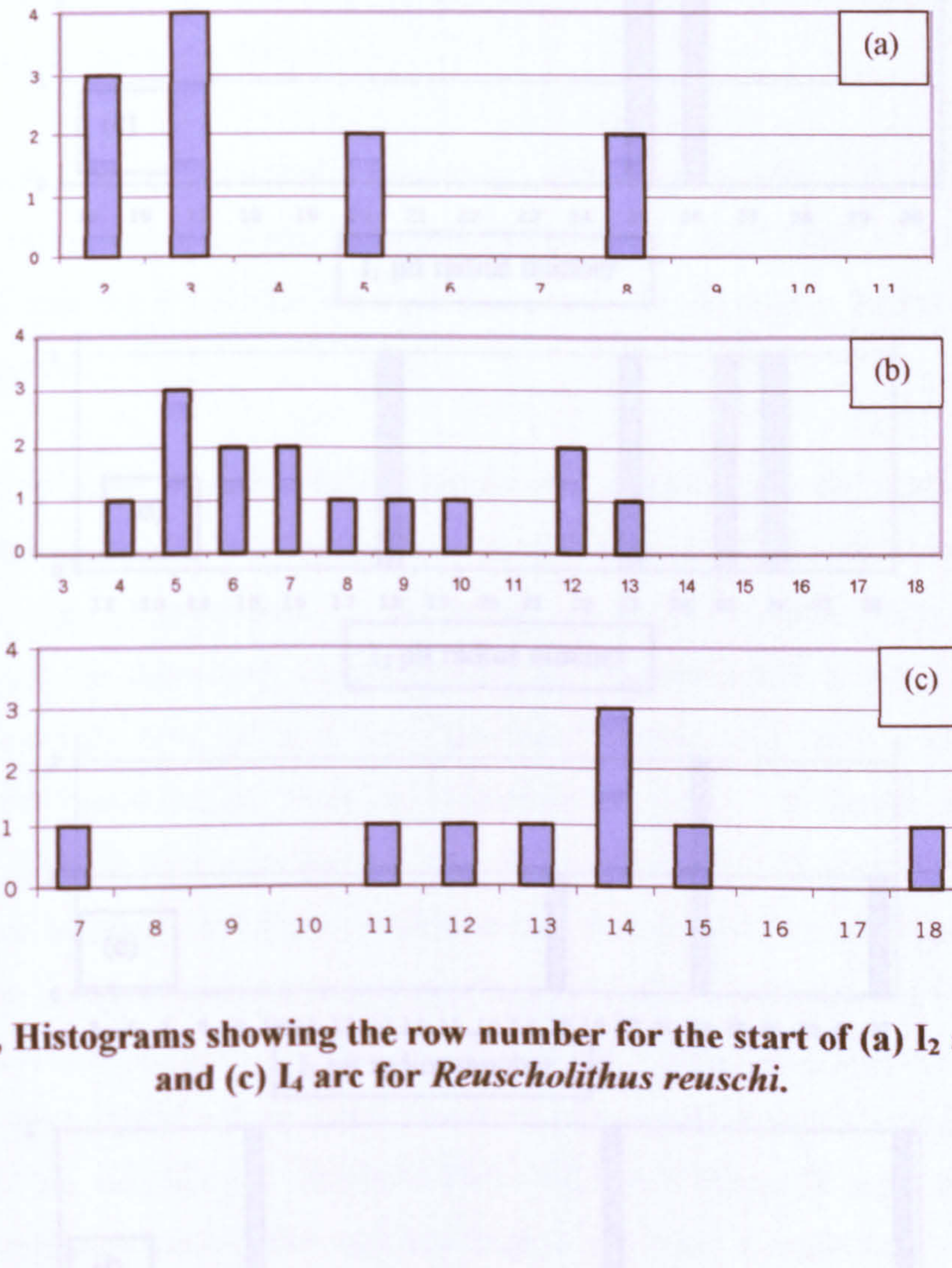
alignment. Girder well defined frontally, narrowing sharply anterolaterally, remaining indistinct to genal angle. No internal pseudogirder. I_1 elevated laterally to posterior.

Remarks. This species shows a range of variation in pit counts, see Text-Figs 4.5,6. Pits are commonly polygonal rather than circular, especially at or near the genal angles. This may be due to the high number of pits and slight deformation during burial. *Reuscholithus* was the last marrolithine for a substantial part of the Caradoc in the Anglo-Welsh area. The subfamily being replaced by the Cryptolithinae, early members of which also show pit disorganisation (Bowdler-Hicks *et al.* 2002). The upper lamella is comparable to *M. elegans*, but is easily distinguished by the absence of inflation, E_2 arc developed past the lateral area and by the much more random distribution of pits. It is possible that *R. reuschi* is a descendant of *Marrolithus* [= *Costonia*] *elegans*.

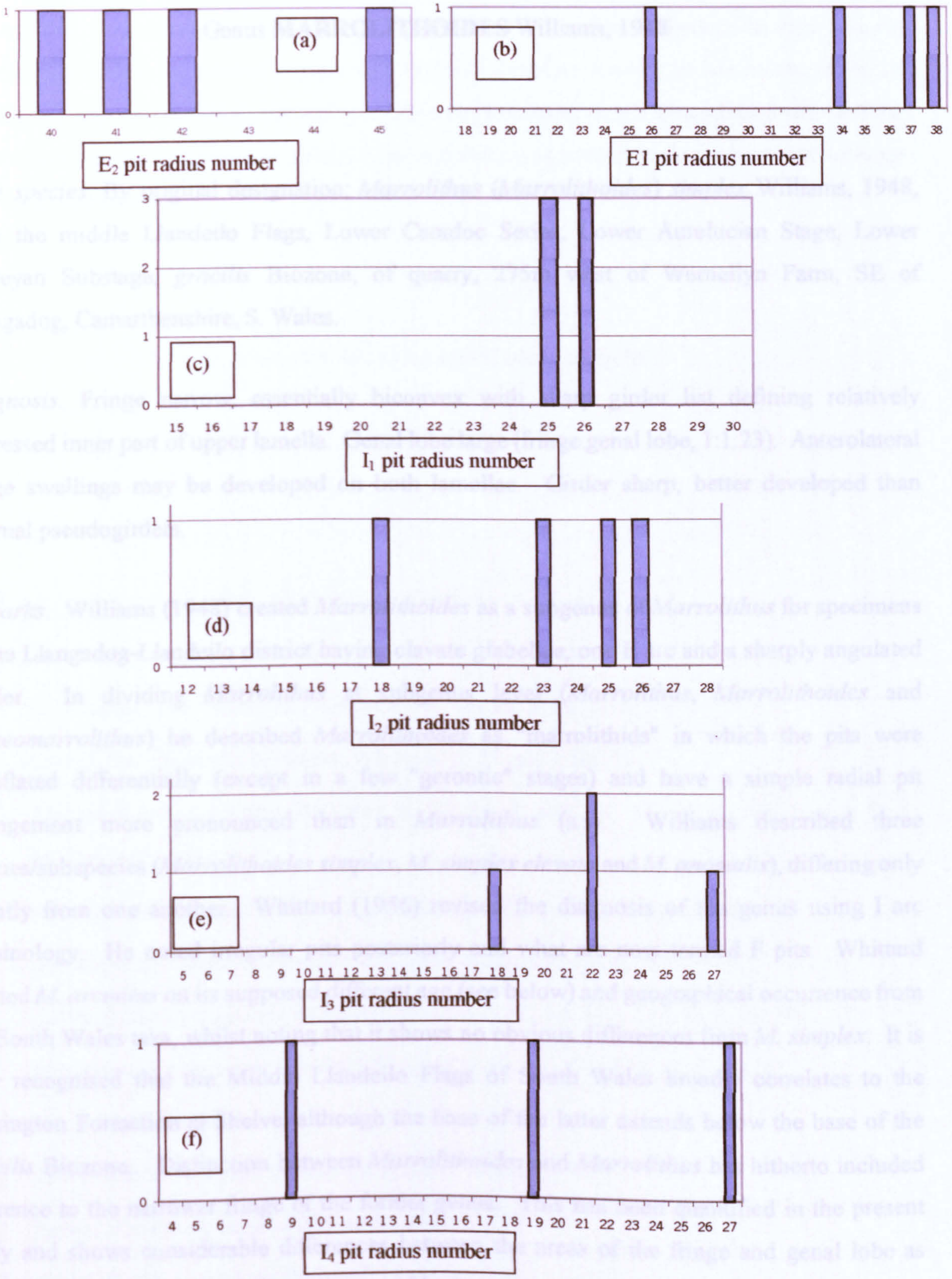
Størmer's (1930) inclusion of *R. reuschi* in the synonymy of *Cryptolithus discors* (Angelin, 1854), [*Broeggerolithus discors* see Bowdler-Hicks *et al.* 2002 and references therein] is not supported here.



Text-Fig. 4.4. Histograms showing (a) I_n pit radius number for *Reuscholithus reuschi* specimens, (b) I_n cut off arc.



Text-Fig. 4.5., Histograms showing the row number for the start of (a) I_2 arc, (b) I_3 arc and (c) I_4 arc for *Reuscholithus reuschi*.



Text-Fig. 4.6. Histograms showing the pit radius number in arcs for *Reuscholithus reuschi*: (a) E_2 pit radius number; (b) E_1 pit radius number; (c) I_1 pit radius number; (d) I_2 pit radius number; (e) I_3 pit radius number and (f) I_4 pit radius number.

Genus **MARROLITHOIDES** Williams, 1948

Type species. By original designation; *Marrolithus* (*Marrolithoides*) *simplex* Williams, 1948, from the middle Llandeilo Flags, Lower Caradoc Series, Lower Aurelucian Stage, Lower Velreyan Substage, *gracilis* Biozone, of quarry, 275m west of Wernellyn Farm, SE of Llangadog, Camarthenshire, S. Wales.

Diagnosis. Fringe narrow, essentially biconvex with sharp girder list defining relatively depressed inner part of upper lamella. Genal lobe large (fringe:genal lobe, 1:1.23). Anterolateral fringe swellings may be developed on both lamellae. Girder sharp, better developed than internal pseudogirders.

Remarks. Williams (1948) created *Marrolithoides* as a subgenus of *Marrolithus* for specimens of the Llangadog-Llandeilo district having clavate glabellae, one E arc and a sharply angulated border. In dividing *Marrolithus* at subgenus level (*Marrolithus*, *Marrolithoides* and *Telaeomarrolithus*) he described *Marrolithoides* as "marrolithids" in which the pits were uninflated differentially (except in a few "gerontic" stages) and have a simple radial pit arrangement more pronounced than in *Marrolithus* (s.s). Williams described three species/subspecies (*Marrolithoides simplex*, *M. simplex elevata* and *M. anomalis*), differing only slightly from one another. Whittard (1956) revised the diagnosis of the genus using I arc terminology. He noted irregular pits posteriorly and what are now termed F pits. Whittard erected *M. arcuatus* on its supposed different age (see below) and geographical occurrence from the South Wales taxa, whilst noting that it shows no obvious differences from *M. simplex*. It is now recognised that the Middle Llandeilo Flags of South Wales broadly correlates to the Rorrington Formation at Shelve, although the base of the latter extends below the base of the *gracilis* Biozone. Distinction between *Marrolithoides* and *Marrolithus* has hitherto included reference to the narrower fringe of the former genus. This has been quantified in the present study and shows considerable differences between the areas of the fringe and genal lobe as measured from photographs of specimens of both genera. *Marrolithoides* shows significantly larger genal lobes, having a fringe:genal lobe ratio about 1:1.23 compared to about 1:0.54 in

Marrolithus. Distorted specimens also show similar ratios. This difference in lobe size may indicate differences in internal organs and possibly therefore feeding or life habits of the two genera and may explain why, although penecontemporaneous, they are associated with different shelf environments and did not coexist. *Marrolithoides* is probably closest to *Hammannaspis* gen. nov. (see below).

Marrolithoides simplex (Williams, 1948)

Text-Figs 4.7-9

1948 *Marrolithus* (*Marrolithoides*) *simplex* Williams; p. 79, pl. 6, fig.5.

1948 *Marrolithus* (*Marrolithoides*) *simplex elevata* Williams; p. 81, pl. 6, fig. 7

1948 *Marrolithus* (*Marrolithoides*) *anomalis* Williams; p. 82, pl. 6, fig. 6.

1956 *Marrolithus anomalis* Williams; Whittard, p. 59, pl. 7, fig. 16.

1956 *Marrolithoides arcuatus* Whittard, p. 64, pl. 8, figs 16, 17; pl. 9, figs 1. *non* fig. 2 [=*Marrolithus favus*]

1975 *Marrolithoides simplex* (Williams); Hughes *et al.*, pp. 572, 573, pl. 8, fig. 98.

1975 *Marrolithoides simplex elevata* (Williams); Hughes *et al.*, pp. 572, 573.

1975 *Marrolithoides anomalis* (Williams); Hughes *et al.*, pp. 572, 573, pl. 8, fig. 99.

1975 *Marrolithoides arcuatus* Whittard; Hughes *et al.*, pp. 572, 573, pl. 8, fig. 97.

1988 *Marrolithoides simplex* (Williams); Morris, p.134.

1988 *Marrolithoides simplex elevata* (Williams); Morris, p.134.

1988 *Marrolithoides anomalis* (Williams); Morris, p.134.

1988 *Marrolithoides arcuatus* Whittard; Morris, p.134.

2000 *Marrolithoides simplex* (Williams); Rushton *et al.*, p. 153, fig. 8.18.

Holotype. Rather flattened internal mould of cephalon showing partial external mould of left lower lamella. By original designation; GSM 75206, from Middle Llandeilo Flags, Lower Caradoc Series, Lower Aurelucian Stage, Velfreyan Substage, lower *gracilis* Biozone, Bethlehem quarry 285m W of Wernellyn Farm, 1 mile SSE of Llangadog, Carmarthenshire, S. Wales.

Material. Over 200 specimens in the National Museum of Wales, Cardiff from Bethlehem Quarry, Llangadog, S. Wales, labelled *Lloydolithus lloydi*, comprising complete and fragmentary articulated specimens, cranidia, cephala, lower lamellae, thoracic segments and rare pygidia, ranging in size from 8-16 mm across widest part of cephaon, majority between 10-14 mm (around 30 complete specimens show only five thorcic segments and are between 10-16 mm). Other samples contain 40 or so well and poorly preserved specimens of complete trilobites, cephala. lower lamellae and pygidia, generally moulds; 9-20 mm width across cephala.

Distribution. Middle Llandeilo Flags Formation, *Marrolithoides simplex* Beds, Lower Caradoc Series, Lower Aurelucian Stage, Lower Velfreyan Substage, lower *gracilis* Biozone: quarry 55m northwest of Keepers Lodge, Dynevor Park, Llandeilo; 91m northwest of St Tyfei's Church, Dynevor Park, Llandeilo; south bank of road cutting Llangadog to Ffairfâch road, Llandeilo; west side of railway cutting 869m south of Ffairfâch Station, Llandeilo; Cennen, south of Ffairfâch, 1.6km southwest Llandeilo; quarry 110m southeast of Bridge House, 3.2km northeast of Llandeilo and Bethlehem quarry, 275m west of Wernellyn Farm, Llangadock, all from Carmarthenshire. Quarry, south of road at west end of Lampeter Velfrey; Kincoed quarry, 600m aouth of Pont-ar-gothi, Dyfed, Wales. Rorrington Shale Formation, Lower Caradoc Series, Lower Aurelucian Stage, Lower Velfreyan Substage, lower *gracilis* Biozone, Meadowtown quarry, Meadowtown, Shropshire, England.

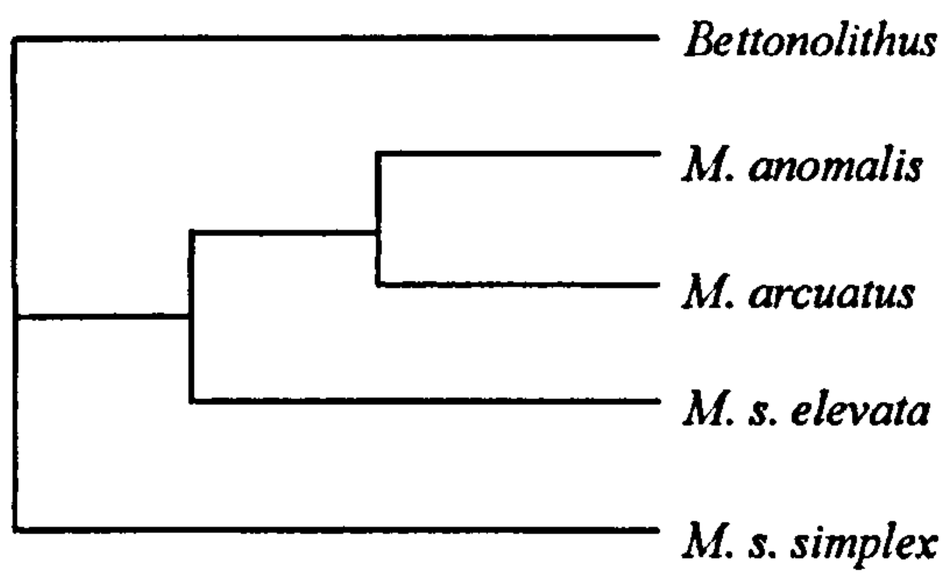
Diagnosis. Subangular cephalic outline. Clavate glabella with two pairs of faint lateral furrows. Genal lobe terminates frontally almost in line with the glabella; fringe:genal lobe ratio about 1: 1.23. Outermost arc E_1, deflected downwards posterolaterally. I_2 arc not continuous frontally; I_1 arc slightly raised posterolaterally with no pit width increase. I_n terminated by short I_3. Small

irregular pits posteriorly. Broad girder list especially frontally. Slight posterior margin extension. Occipital spine.

Description. Cephalic outline is subangular with posterolateral margins tapering outwards slightly. Glabella clavate, faint 1P and 2P lateral furrows; glabellar node prominent. Occipital furrow shallow, preservation and postexhumation damage of specimens has not allowed the presence or absence of an occipital spine to be definitely diagnosed. Genal lobes terminate almost in line with the glabella. Lobes more swollen nearer the fringe. Fringe:genal lobe ratio 1:1.23. Fringe conspicuously narrow frontally to lateral position. I_2 development variable but rarely present mesially. E_1 arc pits well spaced, deflected downwards, particularly posteriorly, broad girder list. I_1 shows slight elevation in posterolateral region where it is defined internally by a very localised first internal list. I_n cut off by I_3 (rarely by a short I_4) and I_3 is overlapped by I_2 in a few specimens. F pits extend frontally (between I_n pits and genal lobe). A small region of irregularly distributed small I pits is also seen posteriorly. Posterior margin shows slight extension with genal angle at approximately the same level as the occipital ring. Six thoracic segments of usual trinucleid type. Subtriangular pygidium with narrow axis showing four faint pleural furrows and three partially developed furrows at the posterior of the pygidial axis.

Remarks. Cladistic analysis based on the type specimens of the "species" currently placed in *Marrolithoides* produces a tree that shows a progression from *M. simplex simplex* to *M. s. elevata* to *M. anomalis* and *M. arcuatus* (Text-Fig. 4.7). The differentiation between the "species" is produced by the difference in the arc terminating In, the number of arcs mesially and the numbers of pits involved in the fringe inflation. However, population sample statistics (Text-Fig. 4.8) show that there is a range of variation within each of these characters in the supposed species and this variation shows considerable overlap indicating that they belong in a single species, for which the name *Marrolithoides simplex* has priority.

The angular fringe outline, I1 arc elevation with no increase in pit diameter and slight invagination of the margin posterolaterally to margin, coupled with its distinct girder extending along the fringe suggest a close relationship to *Hammannaspis* gen. nov. (compare Text-Fig. 4 with Pl. 5).

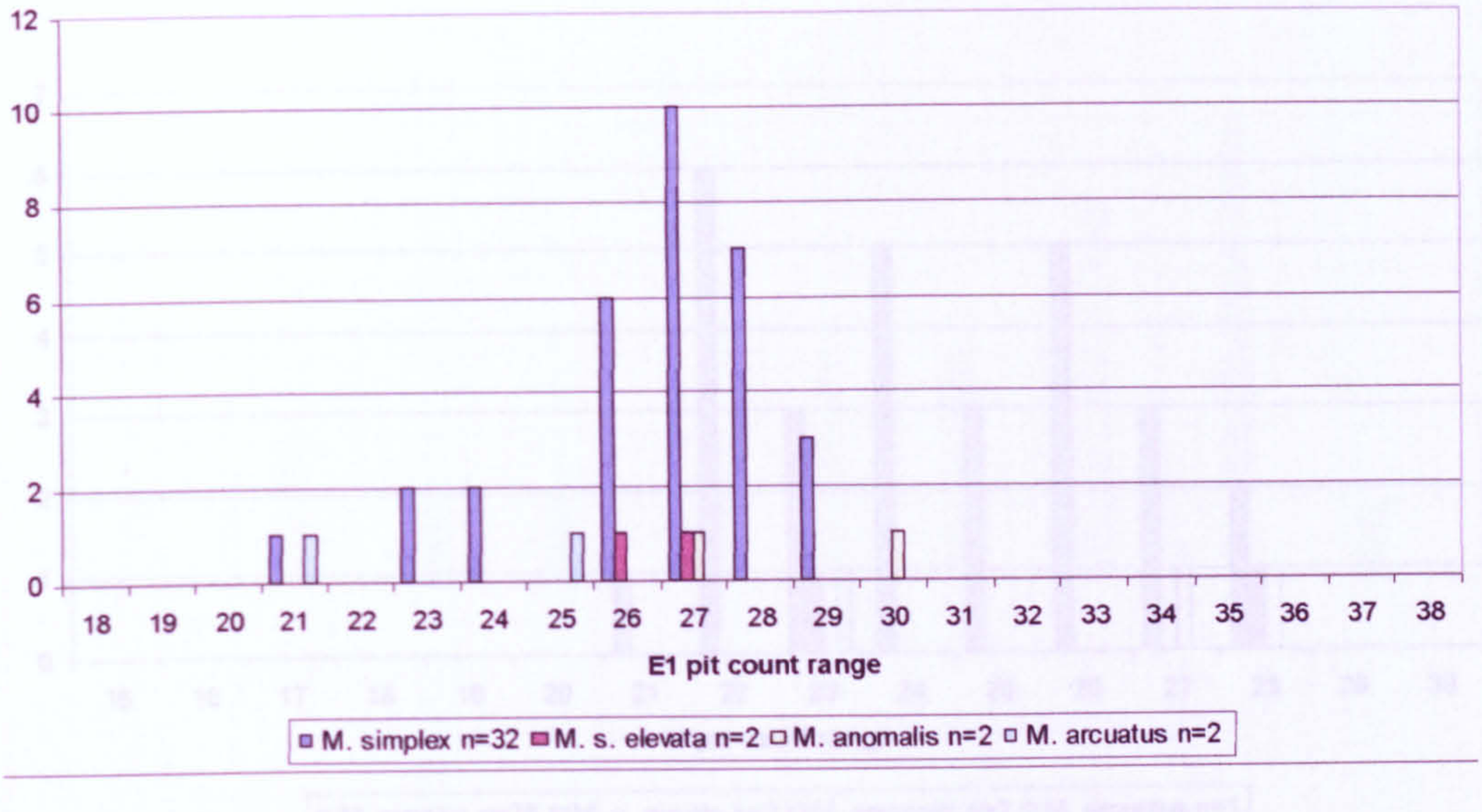


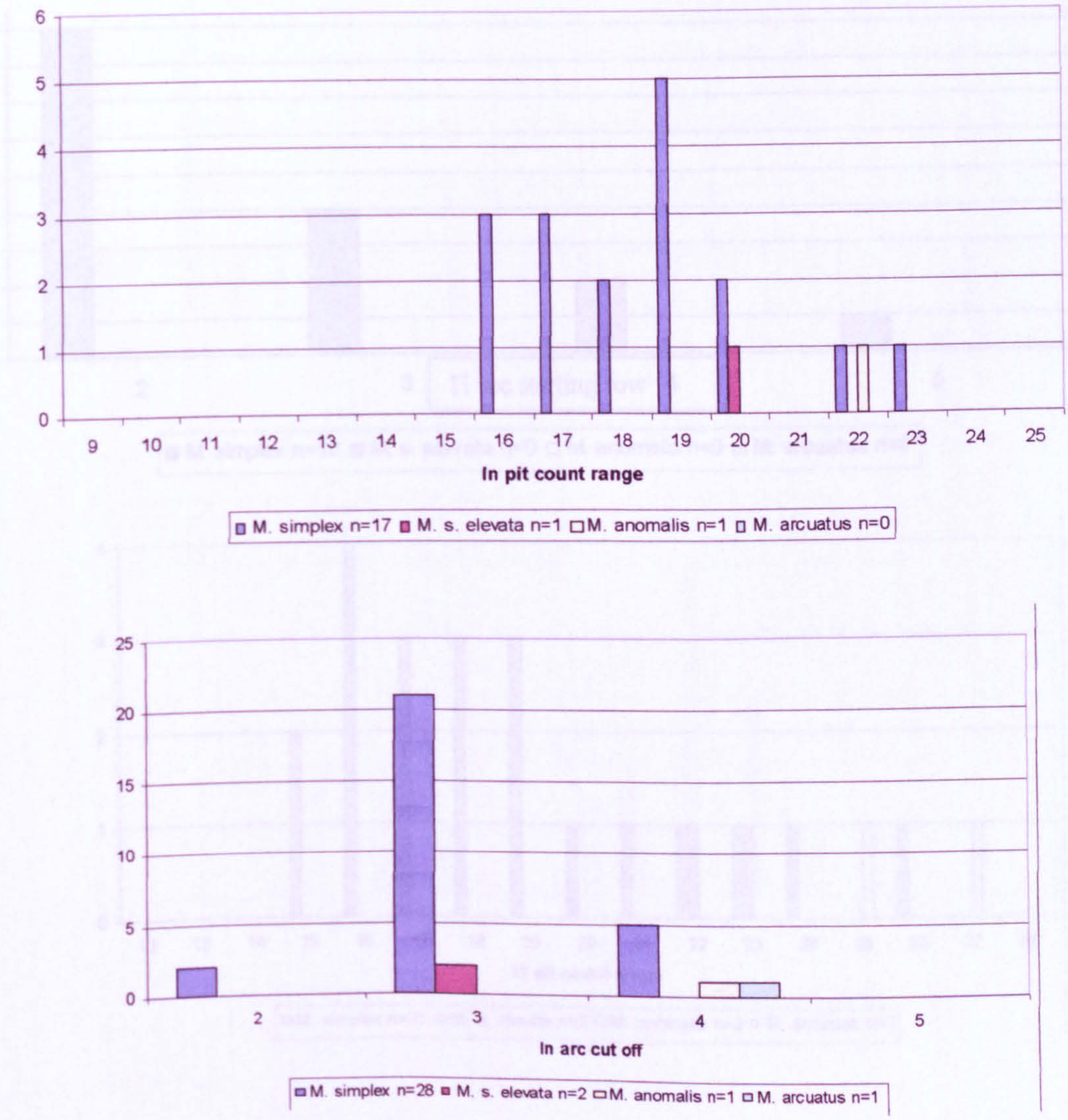
Text-fig. 4.7. Cladistic analysis of the taxa currently included in *Marrolithoides* using the type specimens of the "species". All populations show overlap in the supposedly distinguishing characters and therefore does not reflect the group as a whole. All are included in a single species *Marrolithoides simplex*.

A sample of over 160 *Marrolithoides simplex* fragments of specimens (all erroneously labelled *Lloydolithus lloydi*) ranging in cephalic width from 8-16 mm, from the middle Llandeilo Flags Formation of Bethlehem, Carmarthenshire, South Wales, examined in the present study contained around 60 nearly complete individuals between 10-16 mm across the cephalon. Around 30 of these individuals showed only five thoracic segments, yet show the same size range as those with six thoracic segments. This may suggest that the final meraspid and the first holaspid stage did not represent an increase in overall size.

Marrolithoides simplex is therefore redefined to include *Marrolithoides simplex elevata*, *M. anomalis* and *M. arcuatus*. Specimens originally attributed to *M. anomalis* do show a greater development of I_3 pits frontally and the presence of I_4 but they occur with specimens that would be considered to belong in *M. s. simplex* as originally constrained. Williams (1948) stated that for a short time during the "mid Llandeilo" [now = early Caradoc] the *Marrolithoides simplex* population was replaced by *M. anomalis*. This apparent replacement is a shift in pit counts within the *M. s. simplex* sample and not a different species. Whittard (1956) transferred the holotype of *anomalis* (BGS GSM 75203) and hence the species to *Marrolithus* on account of fringe inflation. Hughes *et al.* (1975) reported Addison's PhD. work on silicified specimens of *M. simplex* showing slight swellings and a well developed girder. They returned *anomalis* to *Marrolithoides*.

The single specimen ascribed to *Marrolithoides* cf. *arcuatus* (see Pl. 1, Fig. 4) by MacGregor (1963) has a lobe to fringe ratio of 0.5:1 and other characteristics of *Marrolithus*. It comes from the same locality as *Marrolithus f. favus* at Nant, Berwyn Hills, Powys, N. Wales and is reassessed here as a distorted specimen of that species. Similarly, the ten incomplete cephala that MacGregor (1963) referred to as *Marrolithoides* sp. are all *Marrolthus f. favus*. The Turkish specimens first ascribed to *Marrolithoides* by Dean (1967) show a fringe: genal lobe ratio of 1:0.56, clearly not that of *Marrolithoides* (1:1.23) (but see below under *Hammannaspis* gen. nov.). Hughes *et al.* (1975) placed all the south-eastern Turkish "*Marrolithoides*" in *Deanaspis*. That view is supported here for *Marrolithoides laticirrus*, *M. inferus* and *M. bedinanensis*, however, *M. orthogonius* is a representative of the new genus *Hammanaspis*.


12
10
8
6
4
2
0
18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38
E1 pit count range
M. simplex n=32
M. s. elevata n=2
M. anomalis n=2
M. arcuatus n=2


6
5
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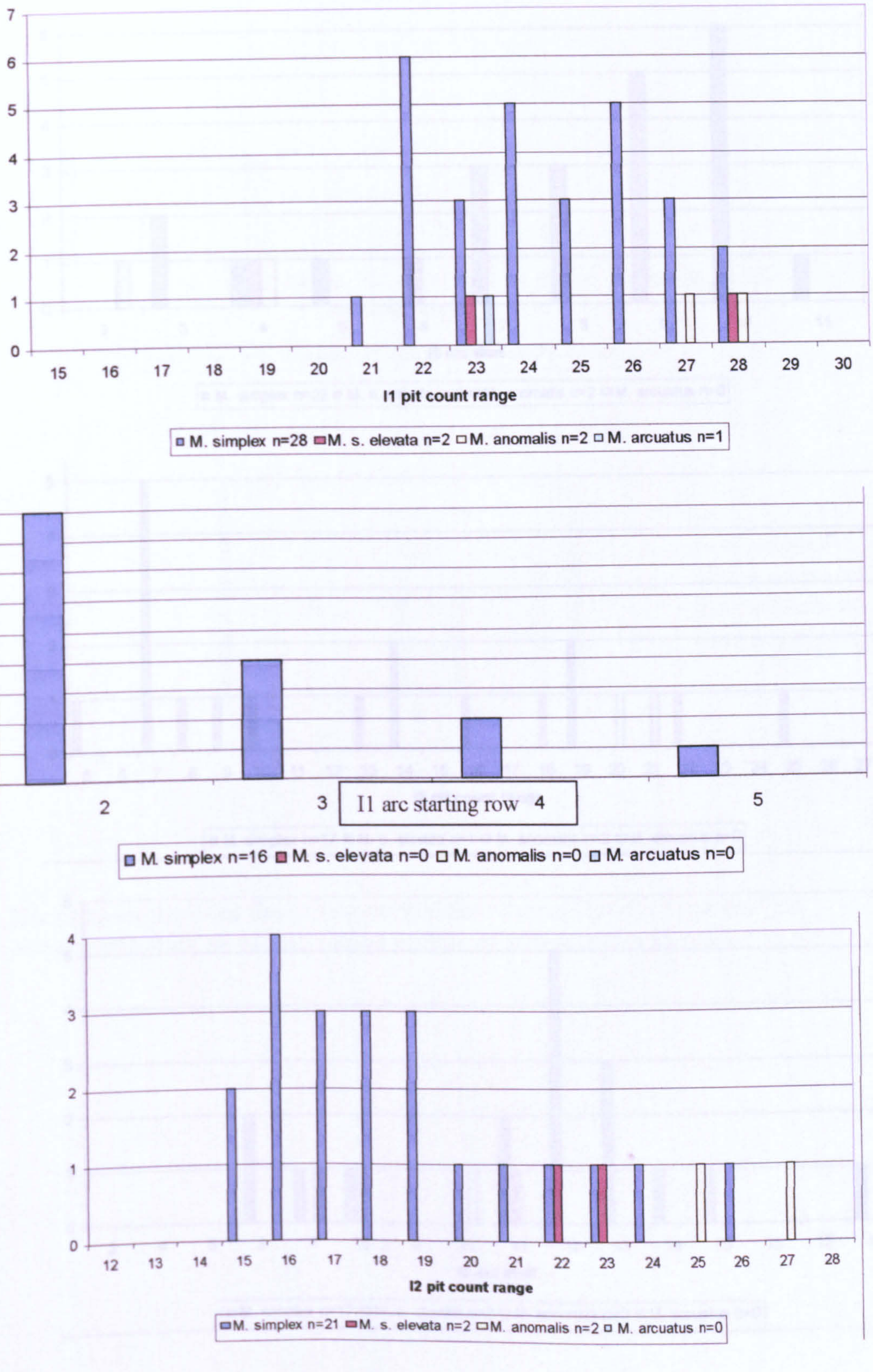
0
9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25
ln pit count range
M. simplex n=17
M. s. elevata n=1
M. anomalis n=1
M. arcuatus n=0

25
20
15
10
5
0
2 3 4 5
ln arc cut off
M. simplex n=28
M. s. elevata n=2
M. anomalis n=1
M. arcuatus n=1


7
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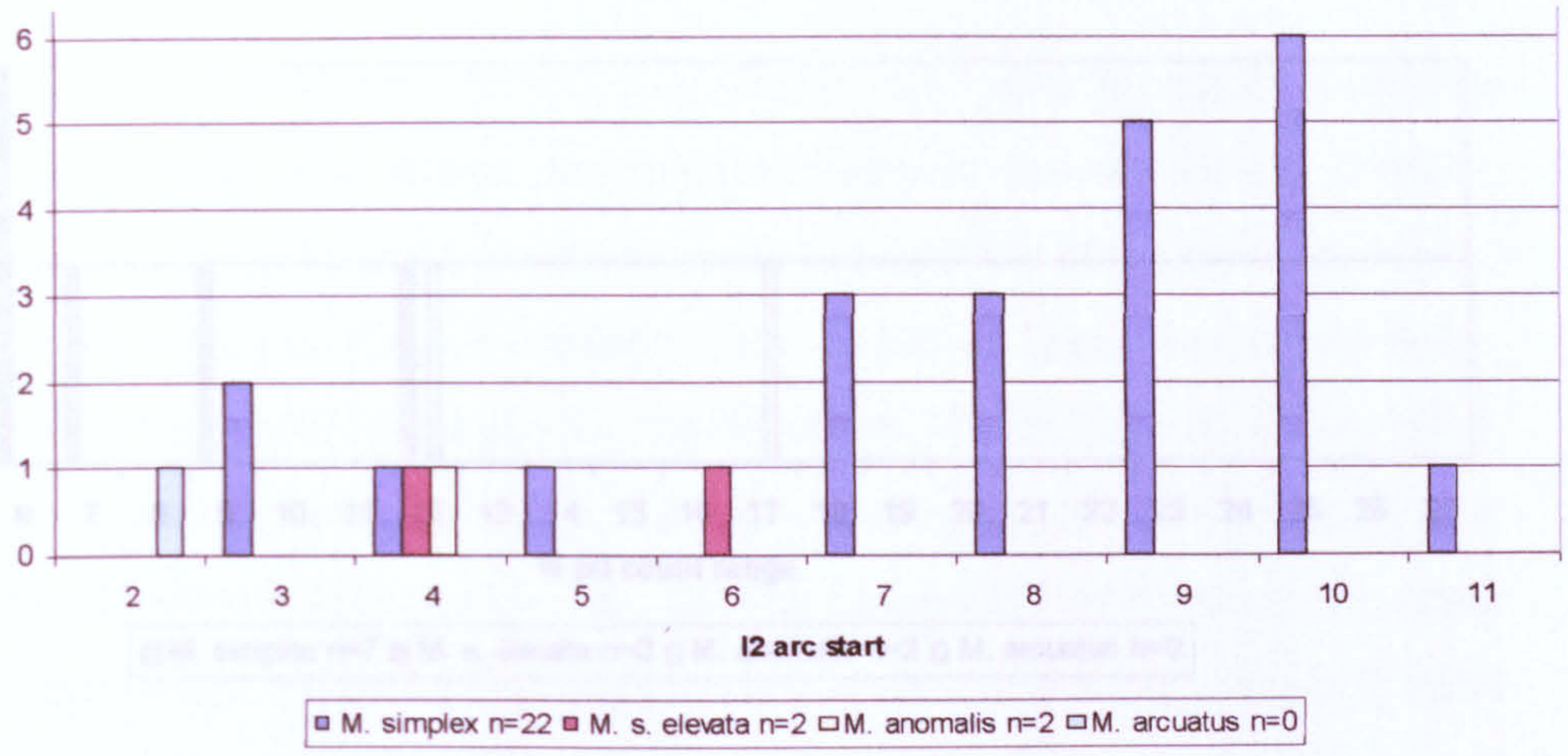
15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
I1 pit count range
M. simplex n=28
M. s. elevata n=2
M. anomalis n=2
M. arcuatus n=1
9
8
7
6
5
4
3
2
1
0
2 3 4 5
I1 arc starting row
M. simplex n=16
M. s. elevata n=0
M. anomalis n=0
M. arcuatus n=0
4
3
2
1
0
12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
I2 pit count range
M. simplex n=21
M. s. elevata n=2
M. anomalis n=2
M. arcuatus n=0


6
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4
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7
8
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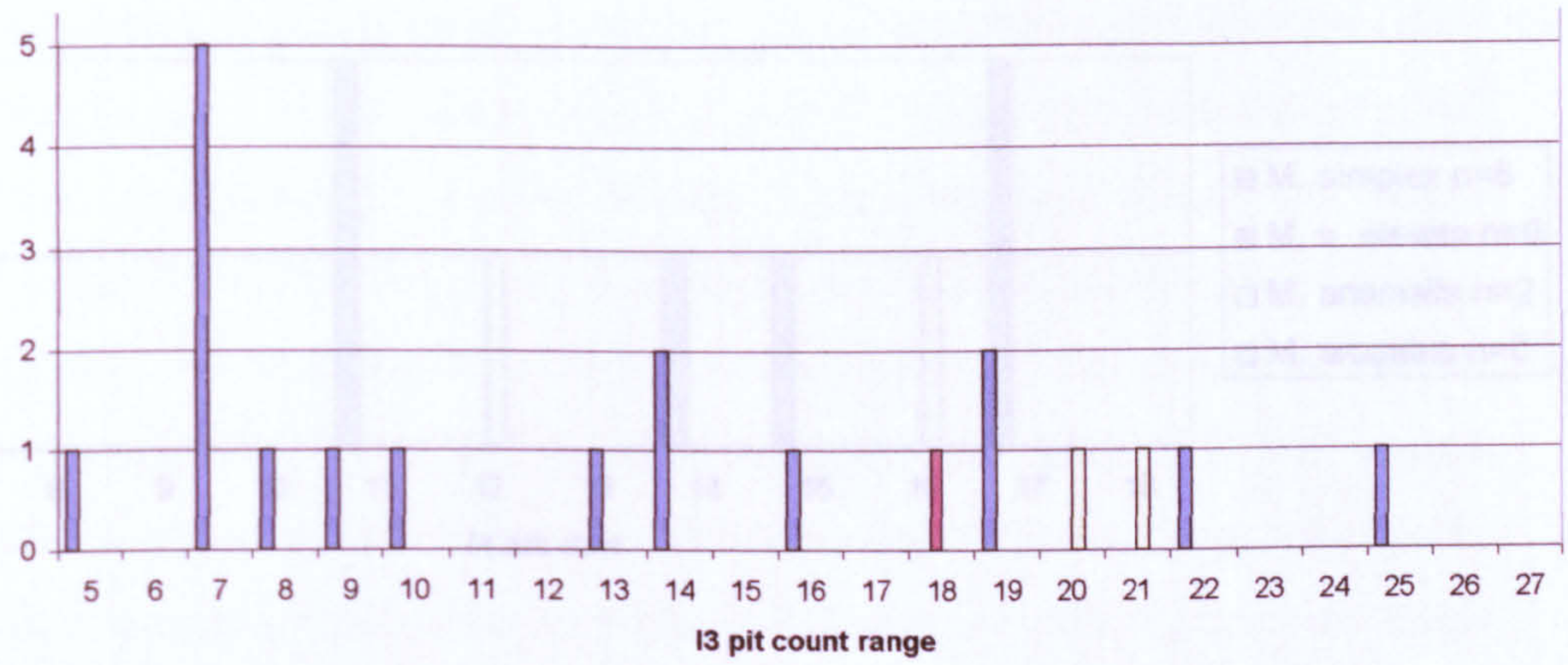
11
l2 arc start
M. simplex n=22
M. s. elevata n=2
M. anomalis n=2
M. arcuatus n=0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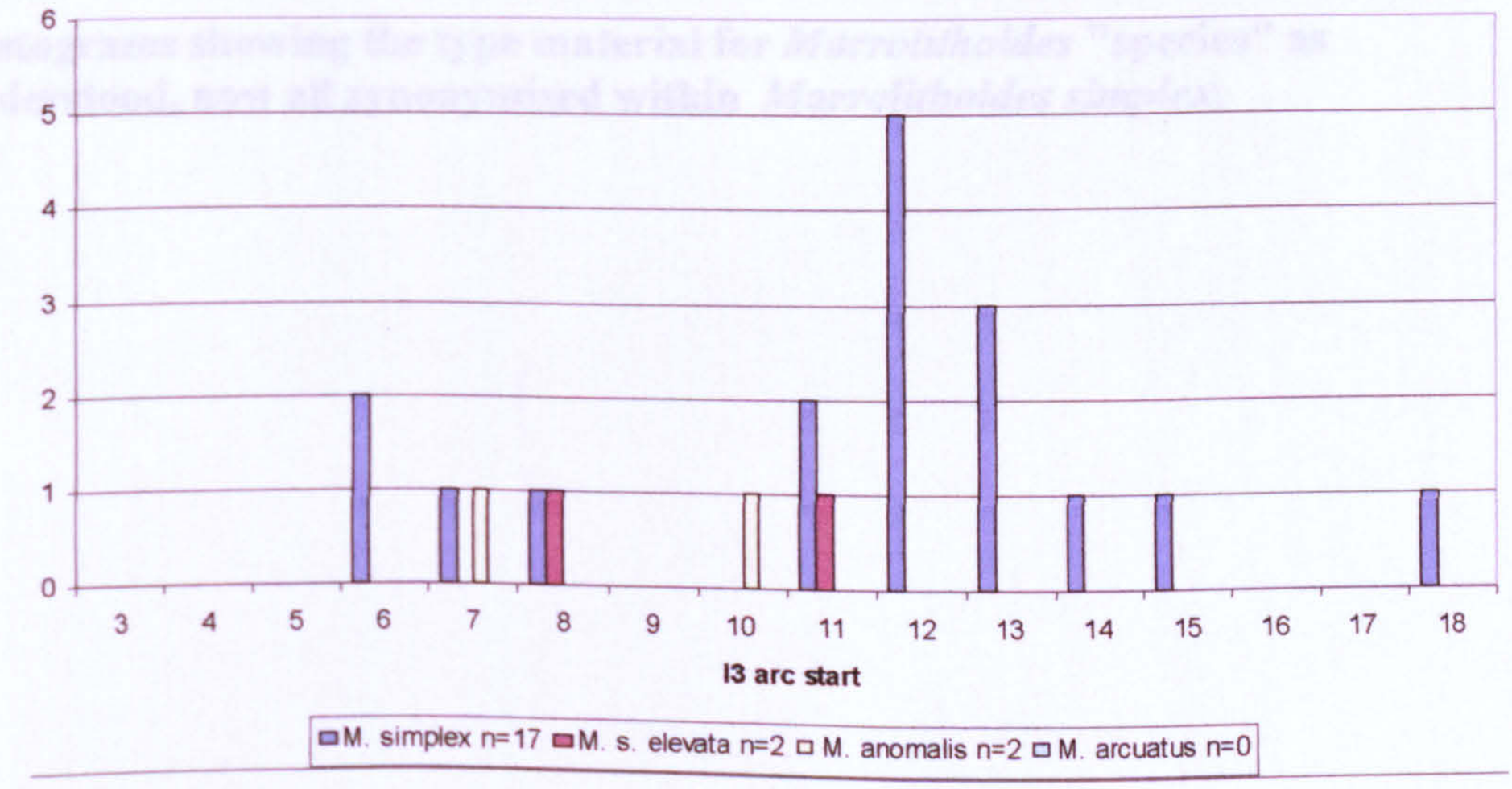
l3 pit count range
M. simplex n=17
M. s. elevata n=1
M. anomalis n=2
M. arcuatus n=0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15
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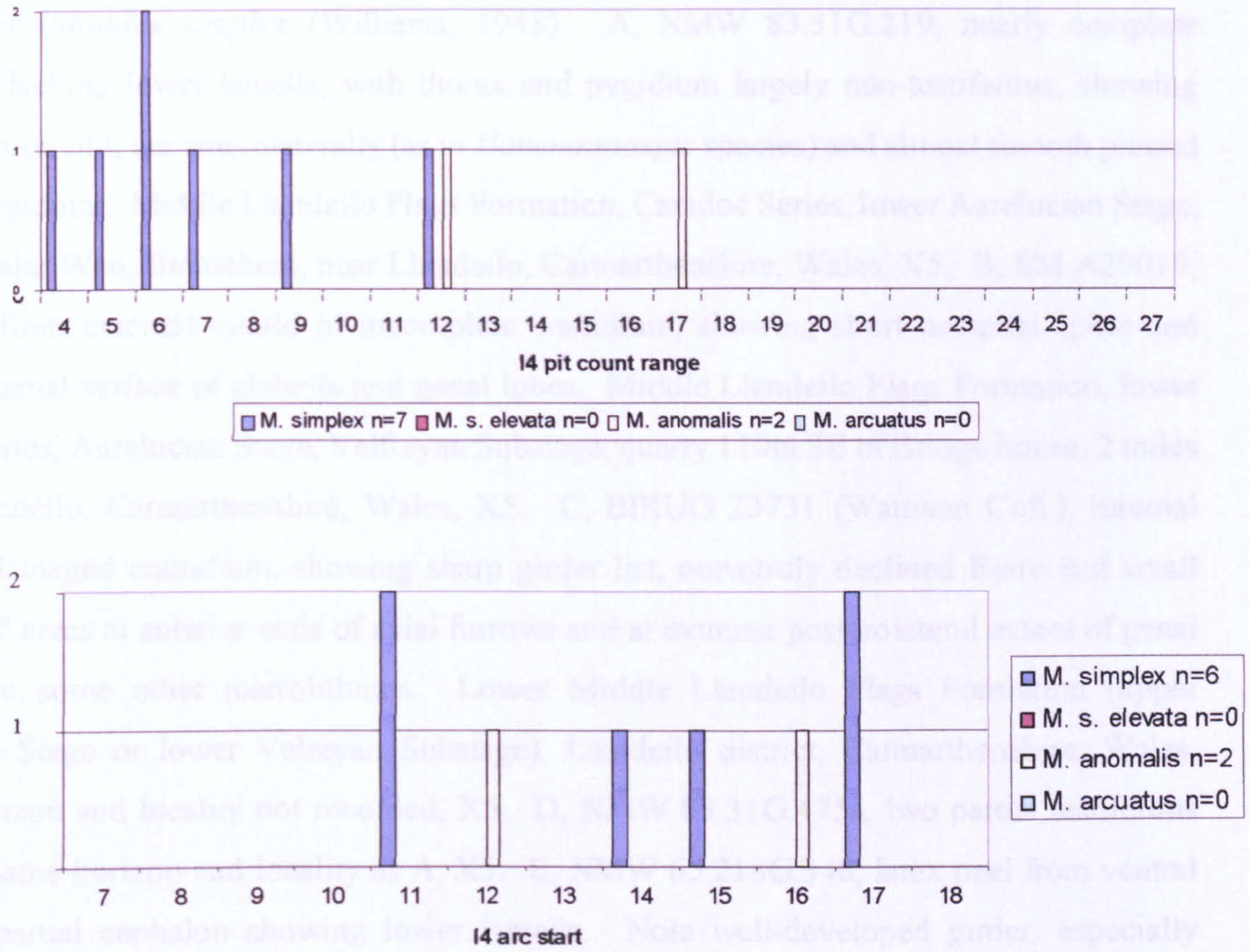
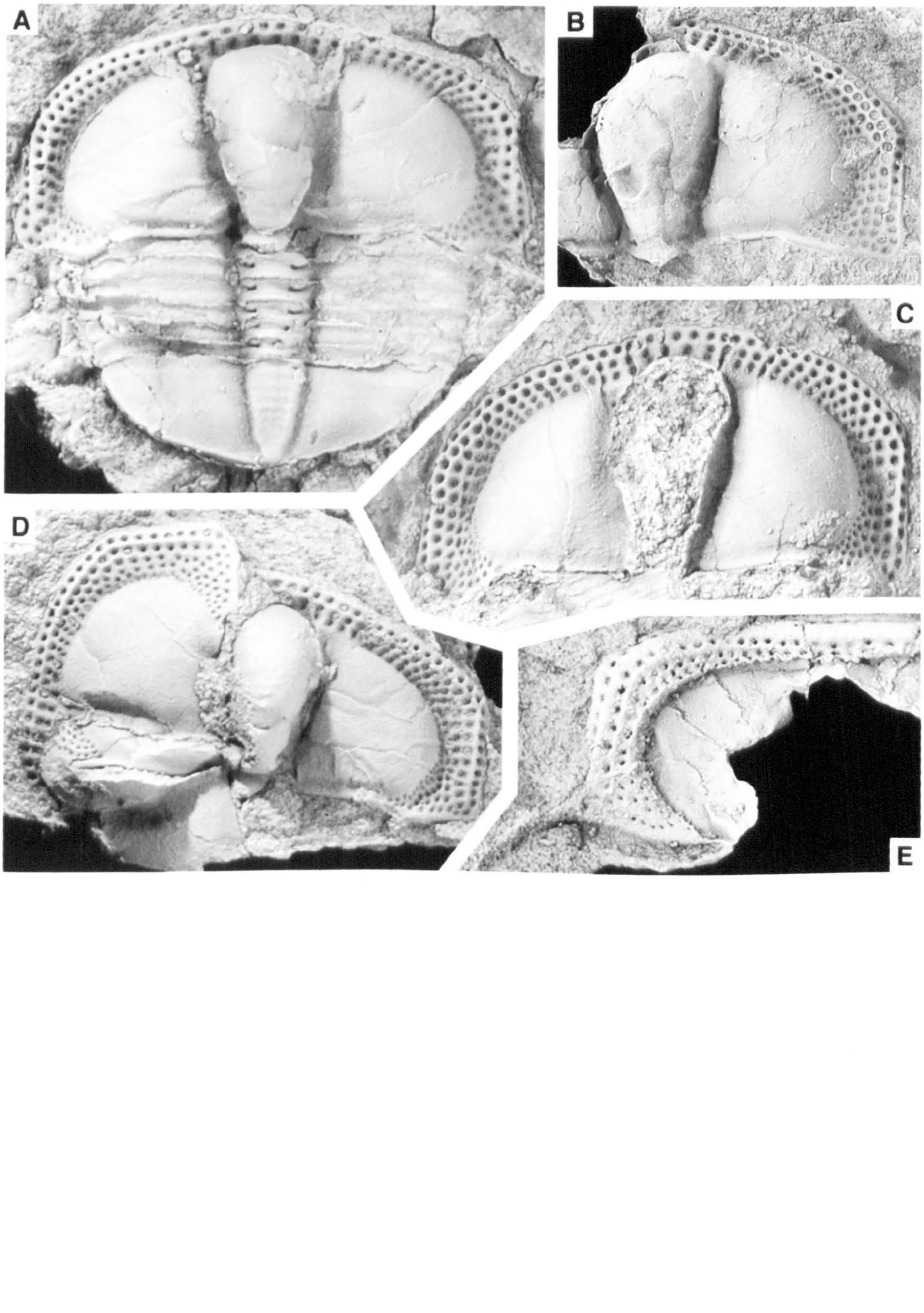
17
18
l3 arc start
M. simplex n=17
M. s. elevata n=2
M. anomalis n=2
M. arcuatus n=0



Text-Fig. 4.8. Histograms showing the type material for *Marrolithoides* "species" as hitherto understood, now all synonymised within *Marrolithoides simplex*.

Explanation of Text-Fig. 4.9

A-E. *Marrolithoides simplex* (Williams, 1948). A, NMW 83.31G.219, nearly complete individual, lacking lower lamella, with thorax and pygidium largely non-testiferous, showing slight elevation of I_1 arc anterolaterally (as in *Hammannaspis* species) and almost smooth pleural lobes on pygidium. Middle Llandeilo Flags Formation, Caradoc Series, lower Aurelucian Stage, quarry at Talar Wen, Bethlehem, near Llandeilo, Carmarthenshire, Wales, X5. B, SM A29019, latex peel from external mould of incomplete cranidium, showing short occipital spine and smooth external surface of glabella and genal lobes. Middle Llandeilo Flags Formation, lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, quarry 110m SE of Bridge house, 2 miles NE of Llandeilo, Carmarthenshire, Wales, X5. C, BIRUG 23731 (Wattison Coll.), internal mould of damaged cranidium, showing sharp girder list, outwardly declined E_1arc and small "sppiculate" areas at anterior ends of axial furrows and at extreme posterolateral extent of genal lobes, as in some other marrolithines. Lower Middle Llandeilo Flags Formation (upper Llandeilian Stage or lower Velreyan Substage), Llandeilo district, Carmarthenshire, Wales. Precise horizon and locality not recorded, X5. D, NMW 83.31G.475a, two partial testiferous cranidia. Same horizon and locality as A, X5. E, NMW 65.218G.348, latex peel from ventral mould of partial cephalon showing lower lamella. Note well-developed girder, especially towards the front and first internal pseudogirder anterolaterally, together with slight anterolateral elevation of arc I_1, a situation very like that seen in *Hammannaspis* species but with extreme narrowness of fringe in *Marrolithoides*, here showing arc I_n truncated by I_2 at about R 21. Same horizon and locality as A, X7.


A
B
C
D
E

Genus **HAMMANASPIS** gen. nov.

Derivation of name: Named for Wolfgang Hammann, renowned German palaeontologist and trilobite researcher, who died in Italy whilst engaged in field work at the age of 60 in 2002. and who also described the species which now forms the type species of the new genus.

Type species. Deanaspis? novaresei Hammann and Leone, 1997, the Portixeddu Formation, horizon Th3a (supposedly Ashgill Series, Pusgillian Stage but possibly slightly older), the pasture at "Ovile Cannamenda", SE of Bacu Abis, Iglesiente-Sulcis autochthon, southern Sardinia.

Distribution. The Portixeddu Formation, (supposedly Ashgill Series, Pusgillian Stage but possibly slightly older), the pasture at "Ovile Cannamenda", SE of Bacu Abis, Iglesiente-Sulcis autochthon, southern Sardinia. From the Nučice ore unit at the base of the Venice Formation and the Zahořany Formation in the Prague Basin. From either the topmost beds of the Izgouiren Sandstone Formation of the First Bani Sandstone Group, Llanvirn Series, upper Llandeilian Stage, or the bottom of the Lower Tiouririne Sandstone Member of the Lower Ktaoua Formation, Ktaoua Clay/Sandstone Group, basal Caradoc Series, Anti Atlas Mountain Region, Morocco. Lower Ktaoua Formation, Schaer, north of Tiona, Tirza District, High Atlas Region. Bedinan Formation (upper *multidens* Biozone) at Sosink, southeastern Turkey.

Generic Diagnosis. Angular fringe; E_1 arc tilted outwards laterally; marked girder list; I_1 arc elevated with no increase in pit diameter; inner surface concave; fringe invagination behind the anterolateral angulation of the fringe margin. Pronounced reticulation on glabella and genal lobes. Girder well developed along entire fringe. Generally no occipital spine.

Remarks. This new genus encompases species previously placed in *Marrolithus* and *Deanaspis* and material from Morocco. These species were poorly resolved within the cladistic analyses (see Section 3.3). The removal of two species, *ornata* and *paulisper*, previously classified as *Marrolithus* has now reduced the stratigraphical range of *Marrolithus* back to the lower Caradoc. The type species was chosen as *H. novaresei* as it is thought to represent the most advanced state of the genus.

Hammannaspis novaresei (Hammann and Leone, 1997)

Plate 5, Figs 9-12

1997 *Deanaspis*? *novaresei* Hammann and Leone, pp. 67-69, text-fig. 16, pl. 27, figs 1, 2.

Holotype. Internal and external mould of almost complete cephalon, IPUM 52133 the Portixeddu Formation, horizon Th3a (supposedly Ashgill Series, Pusgillian Stage but possibly slightly older, the pasture at "Ovile Cannamenda", SE of Bacu Abis, Iglesiente-Sulcis autochthon, southern Sardinia.

Material. Only six well preserved cephala from the type horizon and locality.

Emended diagnosis. Subquadrate cephalic outline; no fringe inflation; no increase in pit diameter; girder list and first internal list bound I1 arc which is slightly elevated anterolaterally; I_2 sulcate mesially; I_n cut-off by I_4 (I_5, if I_5 arc present). Girder distinct along entire fringe; no pseudogirder. No occipital spine

Description. Cephalon subquadrate with fringe invagination behind the anterolateral angulation of the fringe margin; gentle anterior arch. Glabella narrow, clavate, does not protrude onto fringe. Indistinct median tubercle in small individuals. Occipital furrow well incised and bearing deep occipital pits, narrow (sag.) ring; no occipital spine; distinct S1 and S2 lateral furrows. Shallow broad axial furrows; distinct hypostomal pit. Low rounded genal lobes (*sag.* longer than exsag.). Posterior border narrow, no posterior margin extension or genal prolongation. Fringe gently convex postero-laterally. Sharp girder list along entire fringe. E_1 arc tilted downwards. Three arcs in front of the glabella; I_2 commonly sulcate with I_n; I_3 starts at row 5; I_4 starts at row 11; I_5 at row 16 (if present); I_n cut off by generally by I_4 (occassionally by I_5). E_1 pits small, closely; I_1 pits larger than others. No fringe inflation. Good radial alignment of inner pits. Small number of F pits, moderate number of intercalated pits; high number of pits along posterior margin (~12). Lower lamella shows distinct girder over entire fringe, no development of internal pseudogirders. Strong reticulation on glabella and genal lobes.

Remarks. Hammann and Leone (1997, p. 69) noted that there were similarities between this species and "*Marrolithus*" *orthogonius* but stated that it differed in showing no pit enlargmentand I_n and cut off by a higher numbered I arc.

Hammanaspis ornata (Sternberg, 1833)

Plate 5, Figs 1-8

1833 *Trilobites ornatus* Sternberg, p. 53, Pl. 1.

1852 *Trinucleus ornatus* (Sternberg); Barrande, p. 624, pl. 30, figs 51, 52.

1969 *Marrolithus ornatus ornatus* (Sternberg); Přibyl and Vaněk, p. 115, pl. 9, figs 10, 11.

1975 *Marrolithus ornatus ornatus* (Sternberg); Čech, pl. 2, figs 1-4, pl. 4, fig. 4.

1975 *Marrolithus ornatus ornatus* Přibyl and Vaněk, p. 570.

1995 *Marrolithus ornatus* (Sternberg); Shaw, pp, 11, 13, fig. 11- 6, 8-11, fig. 12- 1, 2, 4.

not 1995 *Marrolithus ornatus* (Sternberg); Shaw, fig. 11-5 [= *Deanaspis goldfussii* (Barrande, 1846)]

Neotype. Sternberg's (1833) holotype is lost. Complete specimen designated by Přibyl and Vaněk (1969, p. 115); NM L15216 (old number CD1132), from the Zahořany Formation, upper Caradoc at Praskolesy, Prague Basin.

Distribution. From the Nučice ore unit at the base of the Vinice Formation then a stratigraphical gap until the Zahořany Formation in the Prague Basin. The exact stratigraphic range for many specimens is not clear except those from the Lodenice and Trubin material, these are about 1/3 of the way up in the formation, roughly 100m above the base. Havlíček and Fatka, 1992 interpreted the ore unit as representing deep water and a temperate or polar

environment. The species marks the first obvious appearance of *Marrolithus* in this region at a time when *Deanaspis goldfussi* was living in other environments of the Prague Basin.

Diagnosis. Outline subrectangular. Occipital ring narrow exsagitally, some specimens possess occipital spine, others do not. I_1 pits wider than others and arc elevated from anterolateral position to near posterior of fringe; I_2 not present mesially and not elevated on upper lamella; I_n cut off by I_4 arc; F pits few and no irregular pits posteriorly. Girder distinct laterally; girder and pseudogirder equally developed on remainder of fringe.

Description. Outline subrectangular. Glabella clavate, shallow lateral furrows; exsagittally narrow occipital ring, specimens possess a short occipital spine; reticulation seen on glabella and genal lobes of holaspid individuals. E_1 pits close together posteriorly; I_1 pits wider than others and arc elevated from anterolateral position to near posterior of fringe; I_2 not present mesially and not elevated on upper lamella, I_3 arc starts opposite lateral furrow; I_n cut off by I_4 arc, F pits few and no irregular pits posteriorly. Girder distinct laterally; girder and pseudogirder equally developed on remainder of fringe.

Remarks. Numerous specimens of *Deanaspis goldfussii* in Barrande's collection from the mid 19th Century were incorrectly labelled as *M. ornatus* and some of these specimens have led to recent incorrect descriptions of *M. ornatus* being made (e. g. Shaw 1995, pl. 11, fig. 5 and pl. 12, fig. 2). Přibyl and Vaněk (1969) suggested *M. paulisper* was a subspecies of *M. ornatus*. Shaw separated *M. ornatus* and *M. paulisper* on the grounds that there was insufficient material of the latter species and there was a stratigraphical separation of some 200 m. Two other features that differ between *M. paulisper* than *M. ornatus* is the slightly more swollen glabella and the presence of an occippital spine in the former but not in the latter. Cladistic analysis also shows the close relationship between the two species. In reviewing Shaw (1995) paper Owen and Ingham noted that the Czech forms are stratigraphically higher and have more uniformly developed girders and pseudogirders than does true *Marrolithus* from the British Isles. They raised the possibily that the Czech forms are actually more closely related to *Deanspis*, possibly being local iterative derivatives of that lineage rather than being true *Marrolithus*. The cladistic analysis highlighted doubt over the Bohemian species affiliation to *Marrolithus* as *M. ornatus* and *M. paulisper* appear very labile (see Text-figs 3.4-6) and all material placed herein into *Hammannaspis* show sister group affinites.

Shaw (1995) suggested that *M. bureaui* specimens from the May Fm (Caradoc) in the Amorican Massif and Přibyl and Vaněk's specimens show no obvious differences in fringe structure or pit count, but possess an occipital spine. *M. bureaui* clearly shows two arcs inflated on the upper lamella, no reticultaion on holaspid individuals and shows a strong occipital spine, compare Pl.5, Fig. 1 with Pl. 1, Fig. 1.

Hammannaspis prima sp. nov.

Plate 6, Figs 3-11

Derivation of name. the very first

Holotype. damaged testiferous cephalon, MGS 1484/3 From either the topmost beds of the Izgouiren Sandstone Formation of the First Bani Sandstone Group, Llanvim Series, upper Llandeilian Stage, or the bottom of the Lower Tiouririne Sandstone Member of the Lower Ktaoua Formation, Ktaoua Clay/Sandstone Group, basal Caradoc Series, from Jbel Hajra el Beida, near Taouz, Tafilalt District, Anti Atlas Mountains, southern Morocco, Grid Ref. 606.2/457.3.

Material. Over one hundred testiferous cephala, cranidia, lower lamellae, thoracic segments and pygidia.

Distribution. From either the topmost beds of the Izgouiren Sandstone Formation of the First Bani Sandstone Group, Llanvim Series, upper Llandeilian Stage, or the bottom of the Lower Tiouririne Sandstone Member of the Lower Ktaoua Formation, Ktaoua Clay/Sandstone Group, basal Caradoc Series, west of Tafilalt; Pres du Tizi n'Tankfoult, north of Zagora; north of Jbel Hajra el Beida, near Taouz; section east of Tafilalt; Jbel Hajra el Beida, near Taouz, all Tafilalt District; north of Jbel Tijakhet, Taouz District; Bou Ingarf, Tazzarine district; Jbel bou Isidane, Alnif District. All from the Anti Atlas Mountain Region. Lower Ktaoua Formation, Schaer, north of Tiona, Tirza District, High Atlas Region.

Diagnosis. I_1 arc not complete mesially. I_1 arc elevated laterally to posterolaterally. In cut off by arcs I_4 to I_6; I_5 arcs and above are cut off by neighbouring arc. Marked reticulation on glabella, genal lobes and inside axial furrows. Short occipital spine, no occipital ring. Recorded data; E_1, 24-26 (25); I_1, 19-23 (21.5), starting row, 2-4 (2); I_2, 18-19 (18.5), starting row, 3-5 (4); I_3, 16-17, starting row, 5-6; I_4 14, starting row 18; I_5, 10, starting row 14; I_n, 15-18 (16), cut off by arc, I_4-I_6 (I_5); around 20 F pits.

Description. Subquadrate cephalic outline, some specimens show lateral thickening of the fringe margin producing a "notch". Clavate glabella, shallow 1P lateral furrows, deep occipital pit, no occipital furrow or ring, short broad occipital spine. In small individuals the posterior margin shows thickening posterior to the genal lobes. Genal lobes low and rounded. Distinct girder list, E_1 tilted downwards laterally. I_1 and I_2 pits increase in width laterally, and I_1 arc becomes elevated laterally, inner region of the fringe is concave. I_n cut off by arc I_4 up to I_6. Arcs I_4 inwards are cut off by the next outside arc posteriorly. Very few extra pits posteriorly and low F pit counts (around 20). Strong girder along entire fringe, very broad frontally with faint terrace lines. Strong ridge from genal spine to girder; weaker to first internal pseudogirder. I_1 elevated and wide pits on lower lamella. Strong reticulation on glabella and genal lobes. Pygidium subangular outline, two distinct axial furrows and three, almost straight, faint interpleural furrows.

Remarks. The Moroccan material is mainly in fine grey, mica rich silts and iron rich fine sandstones. The single locality from the High Altas is composed of fine dark clays and silts and contains only fragments of trilobites and complete uncrushed snails. Some of the Moroccan material is preserved well enough to show the fine reticulation along the axial furrow, as seen in *Hammanaspis ornatus*. *H. prima* can be distinguished from *H. ornatus* by its short occipital spine and absent occipital furrow, the higher number of I arcs (generally I_5 or I_6 cf. I_4) and lack of I_1 pits mesially. *H. prima* can be distinguished from the type species, *H. novaesei* by the increase in pit width of I_1 arc to the lateral region, more elevated I_1 arc and narrower fringe posteriorly (allowing I_3 arc to truncate I_4, which truncates I_5 and I_5 truncates I_6, if present) and occipital spine.

Hammanaspis orthogonius (Dean, 1967)

Text-Fig. 4.10

1967 *Marrolithoides orthogonius* Dean; p. 96, pl. 1, figs 1-9.

1975 *Deanaspis orthogonius* (Dean); Hughes *et al.*, p. 574.

Distribution. Only found in the Bedinan Formation (upper *multidens* Biozone) at Sosink, southeastern Turkey.

Remarks. Dean placed *orthogonius* within *Marrolithoides* as the Turkish specimens possess a narrow fringe frontally. The fringe to genal lobe ratio for *H. orthogonius* is 1 : 0.56 compared to *Marrolithoides* ratio of 1 : 1.23, this shows the fringe may appear to have a similar cephalic outline to *Marrolithoides* but it does not possess the characteristic narrow fringe or large rounded genal lobes. The Turkish material does not show localised I_1 arc elevation in the posterolateral area of the upper lamella that is seen in *Marrolithoides*. The strong girder and lack of the first internal pseudogirder; I_1 and I_2 pits larger than others; distinct girder and two pseudogirder lists; I_n terminated by I_4 and small area of irregular pits posteriorly are characters similar to *M. ultimus*. The Turkish species, however does not show I_1 mesially, has low number of F and irregular pits posteriorly and no E_2 pits frontally.

Hammanaspis? paulisper (Přibyl and Vaněk, 1969)

Plate 6, Figs 1, 2.

1969 *Marrolithus ornatus paulisper* Přibyl and Vaněk, pp. 122, 123, pl. 15, figs 4-6, text-fig. 15.

1975 *Marrolithus ornatus paulisper* Přibyl and Vaněk; Hughes et al., p. 570.

1995 *Marrolithus paulisper* Přibyl and Vaněk, p. 13, Figs 11.4, 7.

Holotype. Partial cranidium. By original designation; UUG JV 953 (JV 3307) from the Nucice ore unit, lower Vinice Formation of Chrustenice Mine, Bohemia.

Material. Less than ten specimens of partial moulds of cephala reported.

Distribution. The Nucice ore unit, lower Vinice Formation [= mid Cheneyan] of Chrustenice Mine, Bohemia.

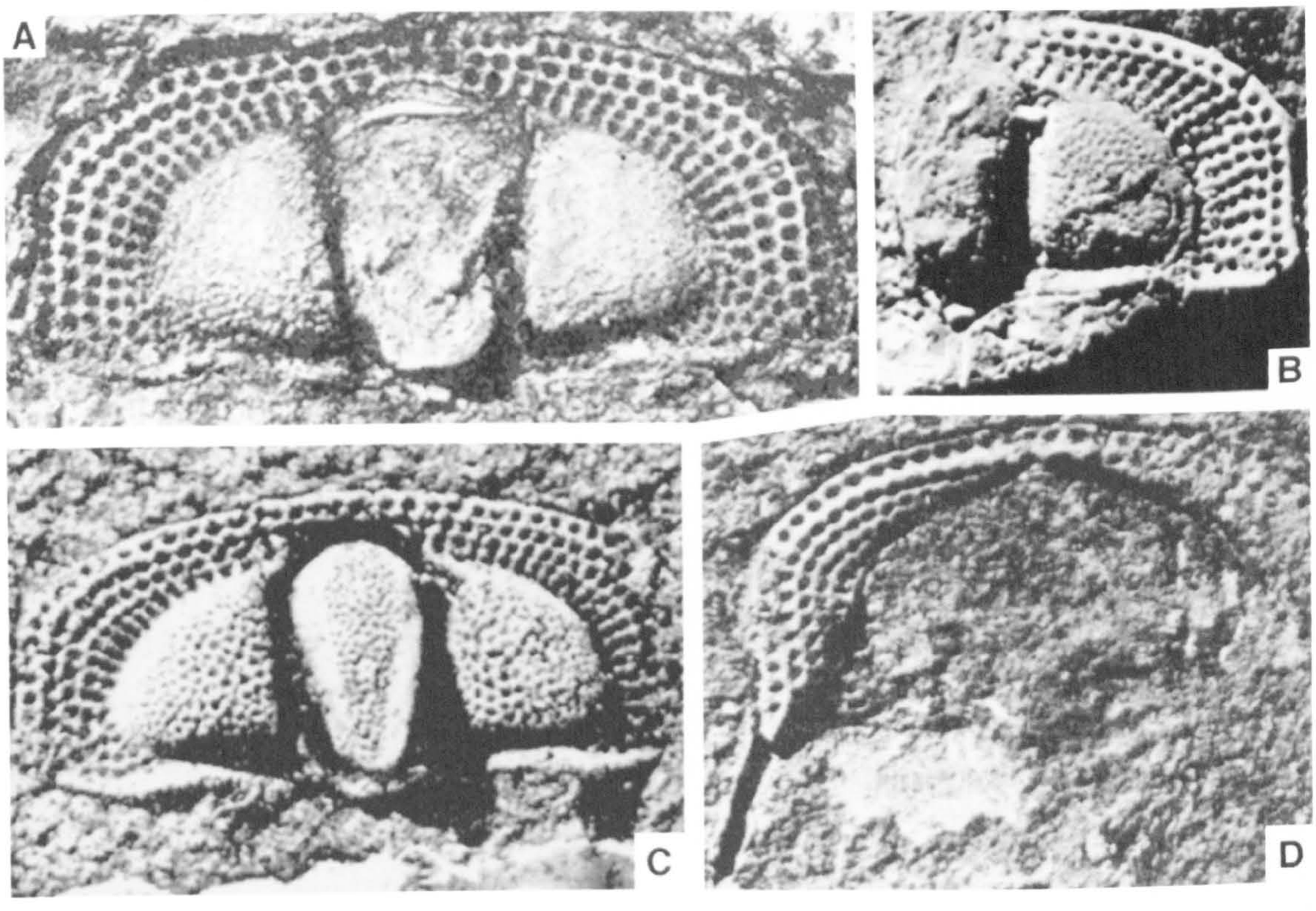
Diagnosis. Subquadrate cephalic outline with fringe invagination behind the anterolateral angulation of the fringe margin. No reticulate sculpture on glabella, genal lobe or axial furrows. I_2 arc not complete mesially. I_1 arc elevated laterally to posterolaterally, inner region of the fringe is concave. Short occipital spine.

Description. Subquadrate cephalic outline with fringe invagination behind the anterolateral angulation of the fringe margin. Clavate glabella, shallow 1P lateral furrows, deep occipital pit, no occipital furrow or ring, stout occipital spine. Genal lobes low and rounded. No reticulate sculpture on glabella, genal lobe or axial furrows. Distinct girder list, E_1 tilted downwards laterally. I_1 arc becomes elevated laterally, inner region of the fringe is concave. I_n cut off by short I_5 arc. Very few extra pits posteriorly and low F pit counts (around 20). Strong girder along entire fringe, very broad frontally with faint terrace lines. Strong ridge from genal spine to girder; weak development of first internal pseudogirder.

Remarks. H. paulisper shows features similar to other *Hammannapis* species, such as the fringe invagination behind the anterolateral angulation of the fringe margin, the slight elevation of the I_1 arc anterolaterally and the "spicular" zones at the end of the axial furrow and near the lateral margin of the genal lobe. The total absence of sculpture impressions on the internal moulds of glabella and genal lobes and the stout occipital spine are not characteristic features of the genus.

Explanation of Text-Fig. 4.10.

A-D. *Hammannaspis orthogonius* (Dean, 1967), gen. nov., taken from Dean (1967, pl. 1), all from the Bedinan Formation, Middle Caradoc Series, locality A.3, east of Sosink, 8km SSE of Derik, South-eastern Turkey. A, BNHM It 1200, holotype, internal mould of cranidium, X6. B., BNHM It 806, small, partial testiferous cranidium showing occipital spine and slight invagination behind anterolateral angle of fringe, X10. C., BNHM It 812, latex peel from external mould of small paratype cranidium, showing coarse reticulate sculpture on genal lobes and along mesial crest of glabella, distinct girder list and outwardly declined E1 arc but virtually no anterolateral elevation of the I1 arc, X10. D., BNHM It 819, internal mould of paratype lower lamella, showing prominent girder anteriorly but little development of first internal pseudogirder, X6.


A
B
C
D

Genus **BETTONOLITHUS** Morris, 1988

[*pro Bettonia* Whittard, 1956 – see Morris 1988, p. 33]

Type species. By original designation; *Bettonia frontalis* Whittard, 1956 [= *Trinucleus chamberlaini* Elles, 1940] from the Llanvirn of Shropshire, England.

Range. Middle Llanvirn, upper Abereiddian, *murchisoni* Biozone of Llandrindod Wells and Builth Wells, Powys, South Wales, Musselwick Bay, Pembrokeshire, South Wales and Shropshire, England.

Emended diagnosis. Semicircular cephalic outline. Glabella clavate with node and three pairs of weak lateral glabellar furrows. First internal list broad, distinct; girder list poorly developed. Girder dominant; first internal pseudogirder prominent. E_1 outermost arc; E_2 commonly developed frontally E_1 and I_1 pits larger than inner pits. Small iregular area of pits posteriorly; no I_2 mesially; I_3 starts well back.

Remarks. Bettonolithus is a monospecific genus, probably closest to *Whittardolithus* from which it is distinguished by the presence of I_2 frontally and the greater number of pits in all arcs. The well developed first internal pseudogirder suggests a possible ancestral relationships to *Deanaspis* (compare Pl. 7, fig. 12 and Pl. 10, fig. 8). Hughes (1971) synonymized all the previously named species within *B. chamberlaini*, an approach which is supported by the present analysis.

Bettonolithus chamberlaini (Elles, 1940)

Plate 7, Figs 8-12, Text-Fig. 4.11.

1940 *Trinucleus chamberlaini* Elles; p. 423, pl. 29, figs 10-12.

1940 *Trinucleus* (*Cryptolithus*) *gibbosus* Elles; pp. 425-426, pl. 31, figs 3-9.

1941 "*Trinucleus*" *chamberlaini* Elles; Whittington, p. 26.

1941 *Trinucleus* (*Cryptolithus*) *gibbosus* Elles; Whittington p. 26.

1941 *Cryptolithus*? *chamberlaini* (Elles); Lamont, p. 449.

1941 *Cryptolithus gibbosus* Elles; Lamont, p. 464.

1956 *Bettonia frontalis* Whittard; pp. 67-68, pl. 9, fig. 7.

1956 *Bettonia chamberlaini* (Elles); Whittard, pp. 67, 69, pl. 9, figs 13-14.

1956 *Bettonia gibbosa* (Elles); Whittard, pp. 67-70, pl. 9, fig. 8.

1956 *Cryptolithus* sp.; Whittard, p. 68, pl. 9, fig. 16.

1956 *Bettonia paucipuncta* Whittard; pp. 68-69, pl. 9, figs 9-11.

1956 *Bettonia irregularis* Whittard; pp. 69-70, pl. 9, fig. 12.

1966 *Bettonia frontalis* Whittard; Whittard, pp. 280-281, pl. 49, figs 1-4.

1971 *Bettonia chamberlaini* (Elles); Hughes, pp. 158-167, pl. 11, figs 9-11, 13-15, pl. 12, figs 1-7, pl. 13, figs 1-8, pl. 14, figs 1-5, 8-10, text-figs 9-11.

1975 *Bettonia chamberlaini* (Elles); Hughes *et al.*, pp. 575-576, pl. 7, figs 86-88, text-fig. 6*c*.

1988 *Bettonolithus chamberlaini* (Elles); Morris, pp. 33-34.

Holotype. Internal mould of partially complete specimen showing dorsal surface and lower lamella. By original designation; BU. 261, from the Camnant Mudstones Formation, lower Llanvirn Series, lower Abereiddian Stage, cliff section on left bank of Howey Brook, Carregwiber, Llandrindod Wells, Powys, Wales.

Distribution. Upper Camnant Mudstones Formation, lower Llanvirn, lower Abereiddian, lower *murchisoni* Biozone [= *D. speciosus* Subzone of Elles 1940] from the cliff section, Howey Brook, Carregwiber, Llandrindod Wells, Powys, Wales. Weston Flag Formation, middle Llanvirn, upper Abereiddian, lower *murchisoni* Biozone from 192 m southeast of Betton Dingle, Meadowtown, Shelve. Builth Volcanic Formation, middle Llanvirn, upper Abereiddian, mid *murchisoni* Biozone from a quarry, 549 m east of Upper Gilwen and the cliff section, Howey Brook,

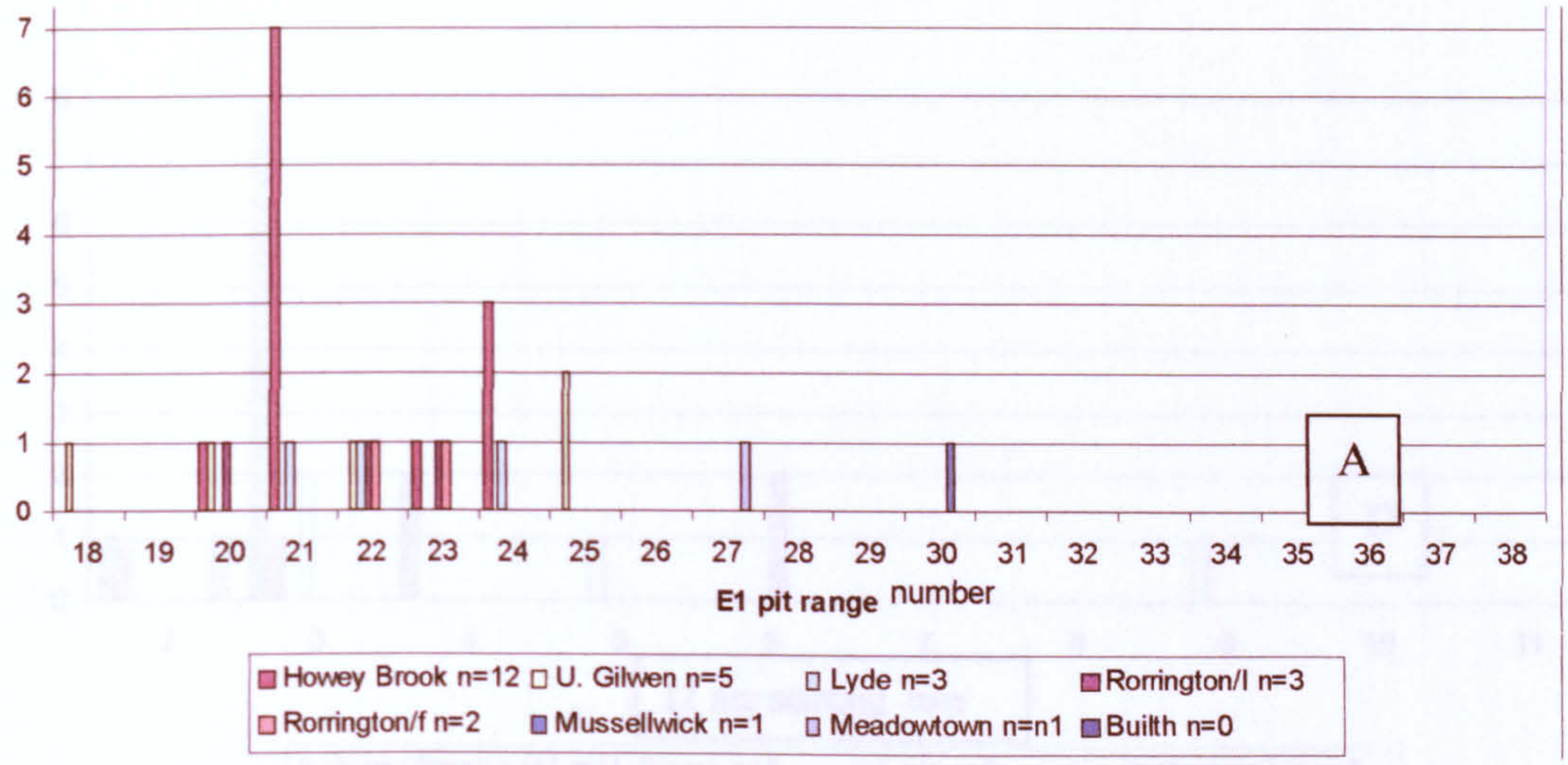
Carregwiber, Llandrindod Wells; small excavation on low hill 200m from Maen Cowyn, 1.25km NE of Llanelwedd Church, Powys. Betton Shale Formation, middle Llanvirn, upper Abereiddian, mid *murchisoni* Biozone from the stream section south of Holywell and Whitehouse Brooks, Rorrington, south side of lane leading to Lyde, 155 m southeast of Mincop and stream section 302 m west south west of Little Weston, Shropshire.

Emended Diagnosis. Semicircular to subrectangular cephalic outline. E_2 commonly developed frontally. I_2 present frontally but not continuous in front of glabella; I_n cut off by I_3 arc posterolaterally. First internal list broad, distinct; girder list poorly developed. Girder dominant; first internal pseudogirder prominent. Glabella clavate with three pairs of weak lateral glabellar furrows. Recorded pit counts: E_2, 0-7; E_1, 20-27 (mean 22); I_n, 9-16 (13); I_1, 16-25 (21); I_2, 12-27 (19); I_3, 5-18 (11). F pits, 11-26.

Description. Cephalic outline, semicircular if E_2 pits present frontally, subrectangular if no E_2 present. Glabella clavate, glabellar node at mid-length, three pairs of faint furrows. Occipital furrow shallow, narrow ring tapering evenly rearwards into a long spine. Genal lobes terminate frontally behind the level of the front of the glabella, deep broad axial furrows. E_1 and I_1 pits larger than other I pits. I_2 not present mesially but generally starts before genal lobes. I_3 short and cuts off I_n. Recorded pit counts: E_2, 0-7; E_1, 20-27 (mean 22); I_n, 9-16 (13); I_1, 16-25 (21); I_2, 12-27 (19); I_3, 5-18 (11). F pits, 11-26. Small posterior area of irregular pits and F pits. Posterior margin shows extension and no genal prolongation.

Six segments in thorax (in holaspid). Subtriangular pygidium shows distinct axial furrows and interpleural furrows which curve rearwards close to the pygidial margins, the angle of curvature increases posteriorly (see Pl. 7, Fig. 10).

Remarks. Hughes (1971) carried out a detailed study of *Bettonolithus chamberlaini* and synonimized the other four species previously ascribed to *Bettonolithus* [as *Bettonia*] by Whittard (1956) within it. This is supported here.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E1 pit range number
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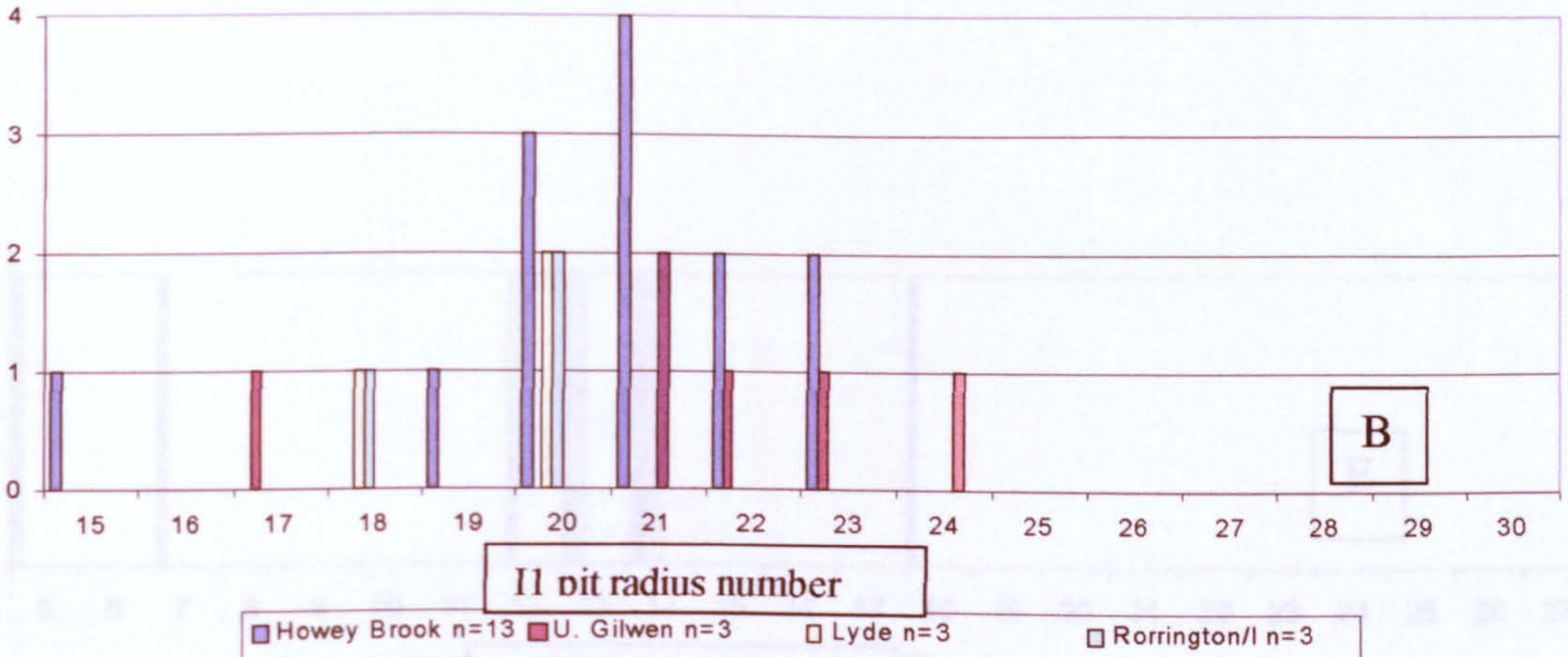
U. Gilwen n=5
Lyde n=3
Rorrington/l n=3
Rorrington/f n=2
Mussellwick n=1
Meadowtown n=n1
Builth n=0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B
I1 pit radius number
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U. Gilwen n=3
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Rorrington/l n=3
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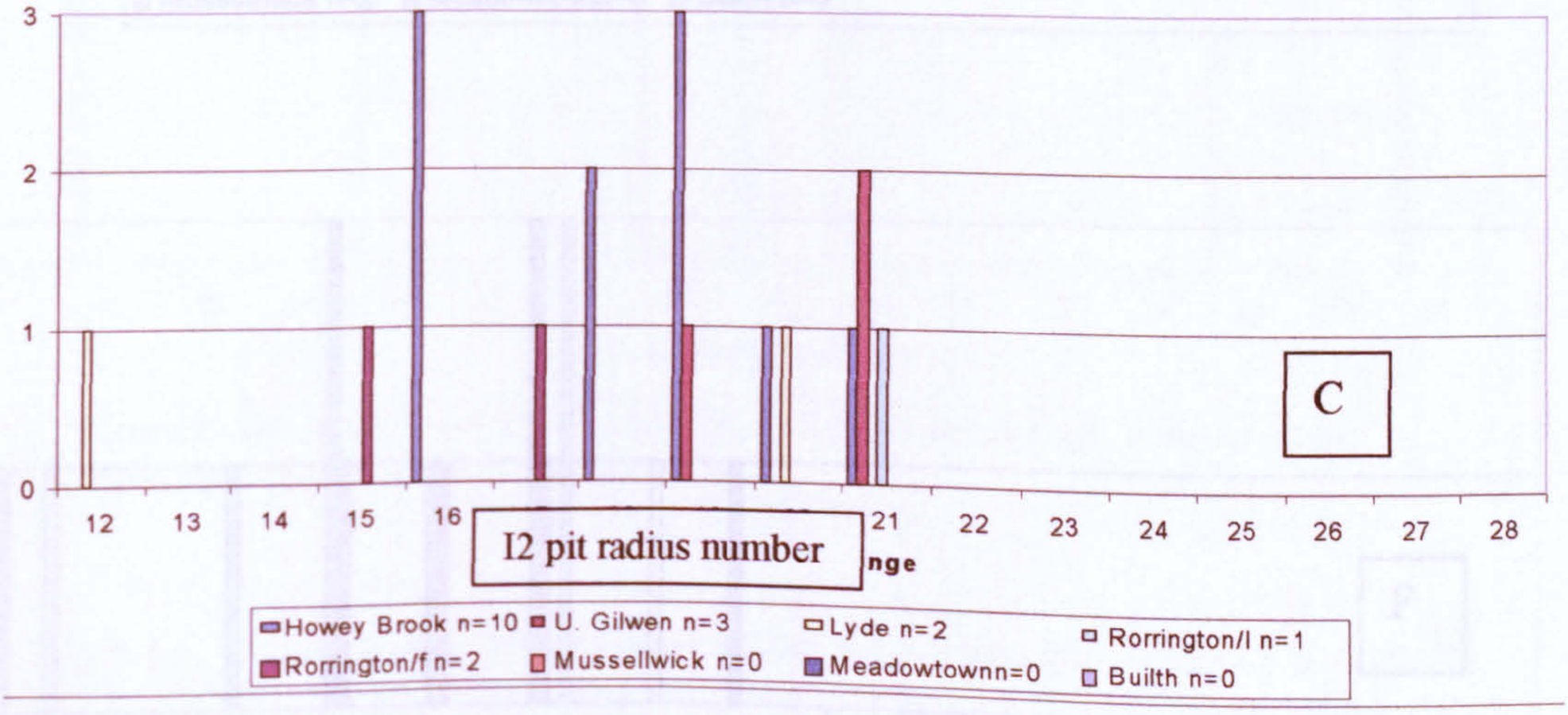
Meadowtownn=0
Builth n=0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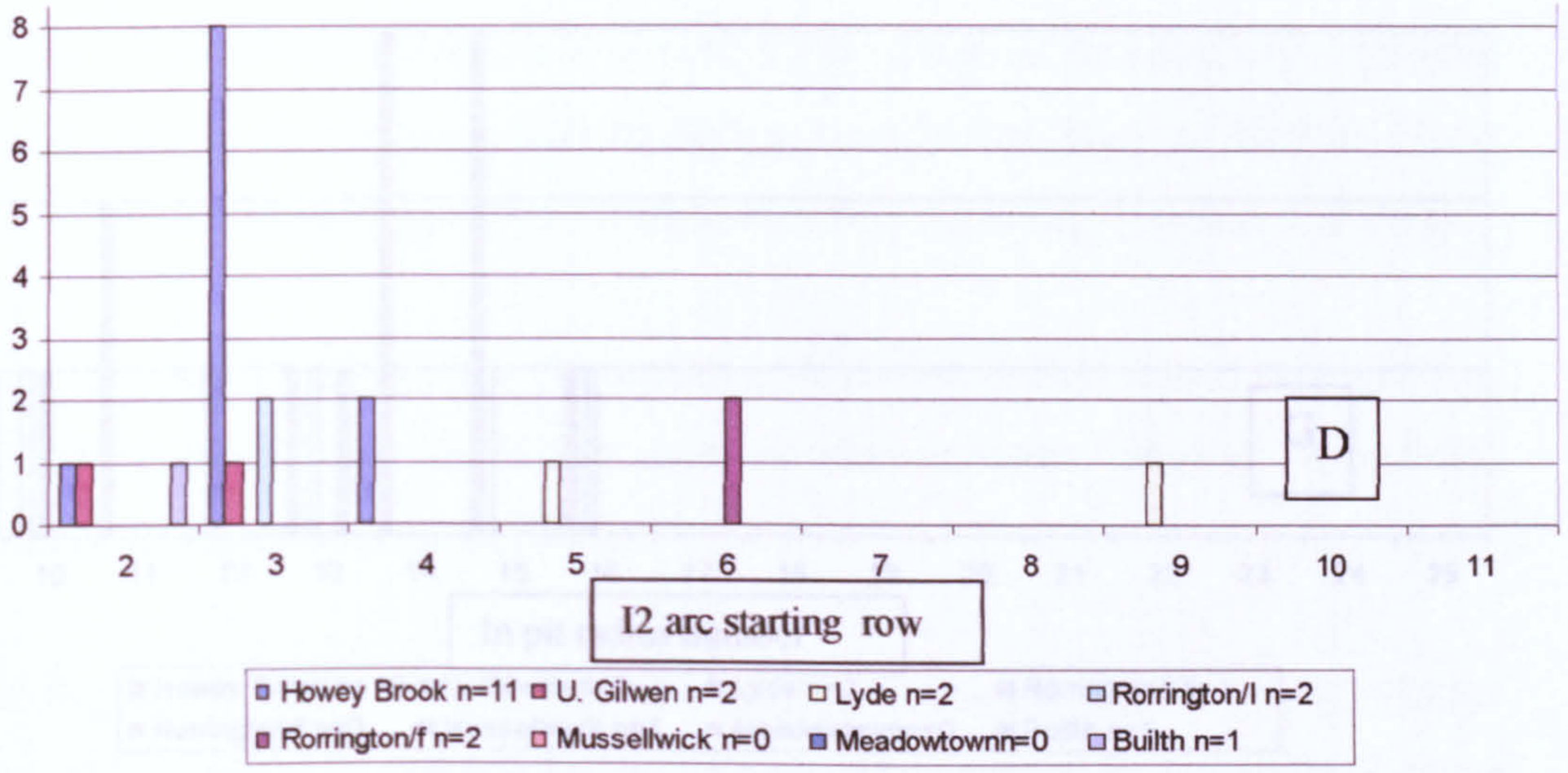
Builth n=0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Mussellwick n=0
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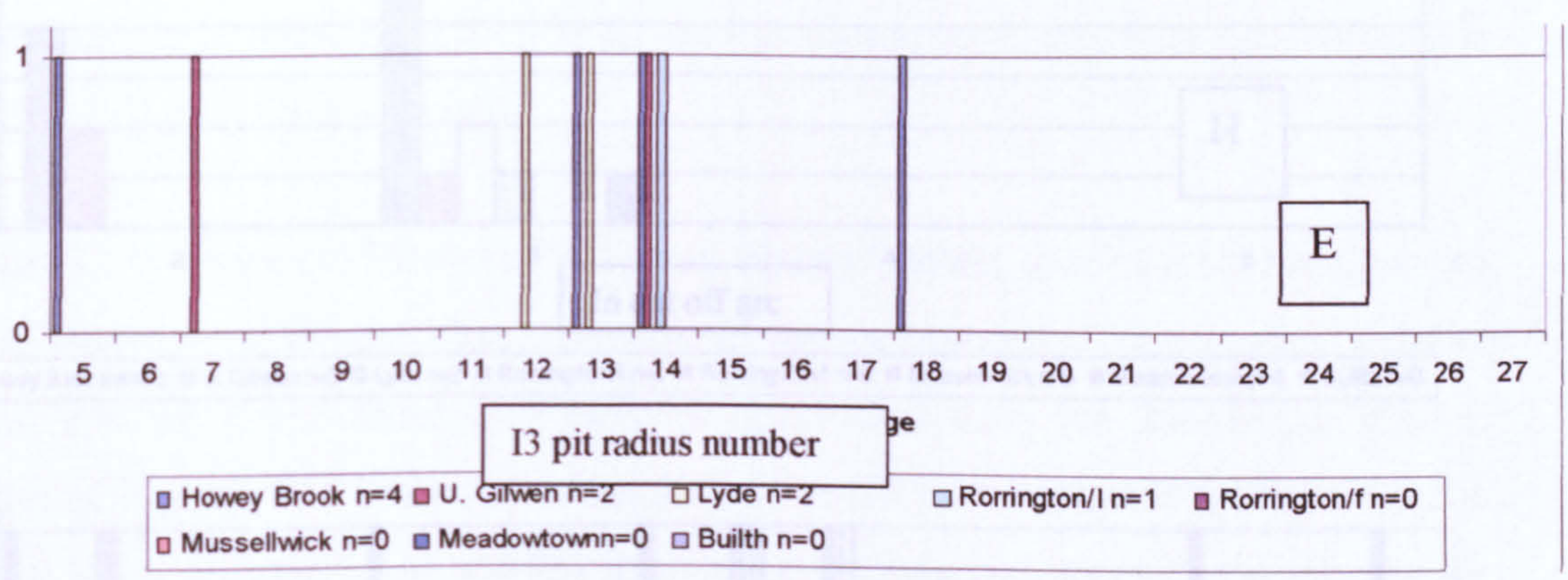
Builth n=1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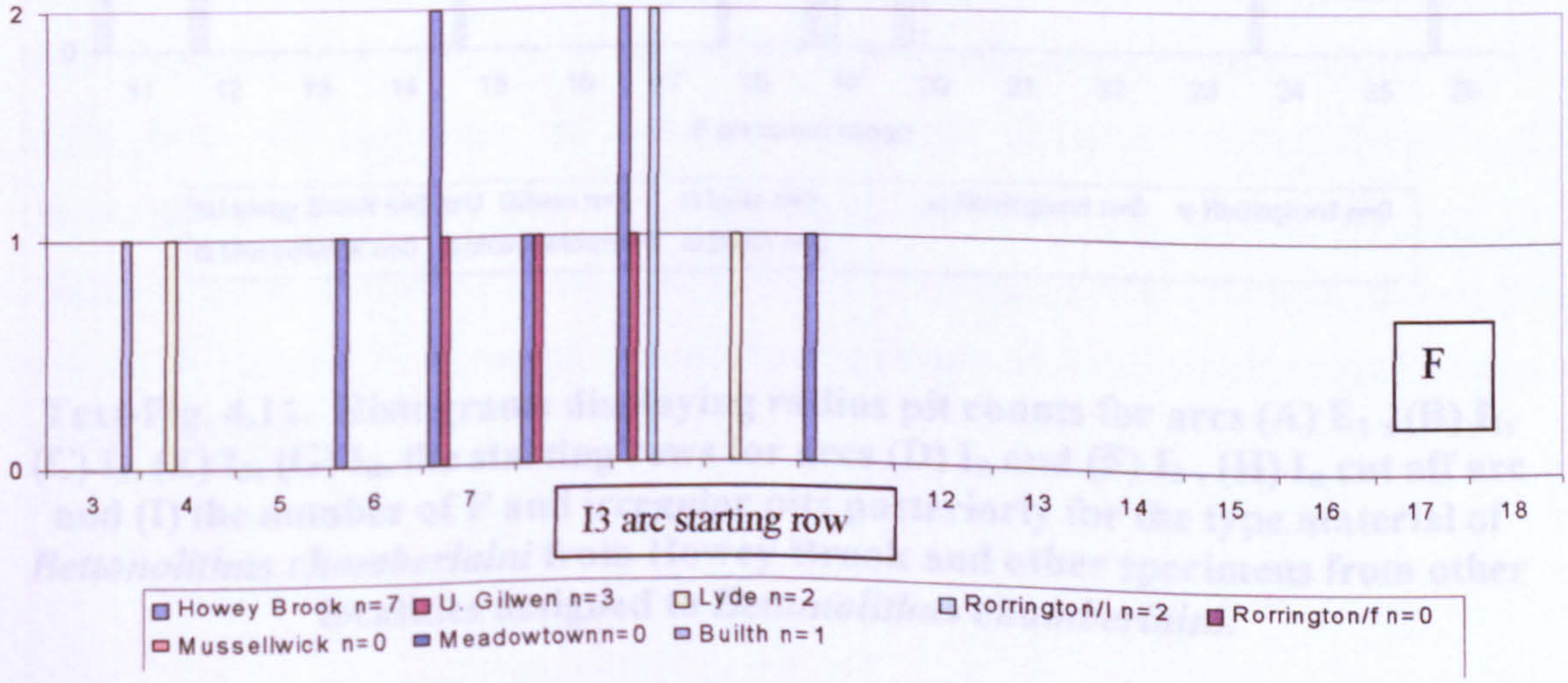
I3 pit radius number
Howey Brook n=4
U. Gilwen n=2
Lyde n=2
Rorrington/l n=1
Rorrington/f n=0
Mussellwick n=0
Meadowtownn=0
Builth n=0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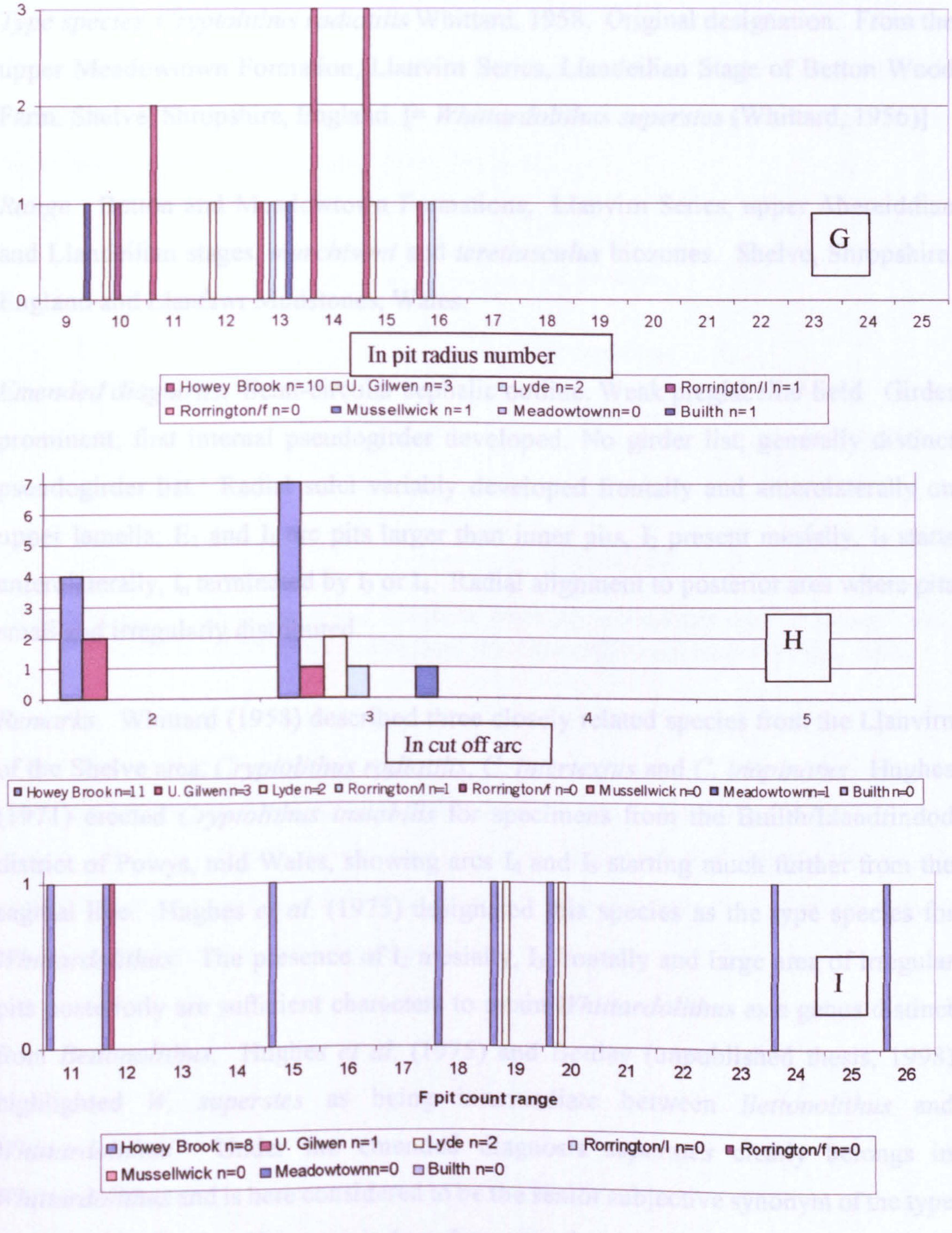
I3 arc starting row
Howey Brook n=7
U. Gilwen n=3
Lyde n=2
Rorrington/l n=2
Rorrington/f n=0
Mussellwick n=0
Meadowtownn=0
Builth n=1



Text-Fig. 4.11. Histograms displaying radius pit counts for arcs (A) E_1 , (B) I_1, (C) I_2, (E) I_3, (G) I_n, the starting rows for arcs (D) I_2 and (F) I_3 , (H) I_n cut off arc and (I) the number of F and irregular pits posteriorly for the type material of *Bettonolithus chamberlaini* from Howey Brook and other specimens from other localities assigned to *Bettonolithus chamberlaini*.

Genus **WHITTARDOLITHUS** Hughes, Ingham and Addison, 1975

Type species. *Cryptolithus radiatilis* Whittard, 1958. Original designation. From the upper Meadowtown Formation, Llanvirn Series, Llandeilian Stage of Betton Wood Farm, Shelve, Shropshire, England. [= *Whittardolithus superstes* (Whittard, 1956)]

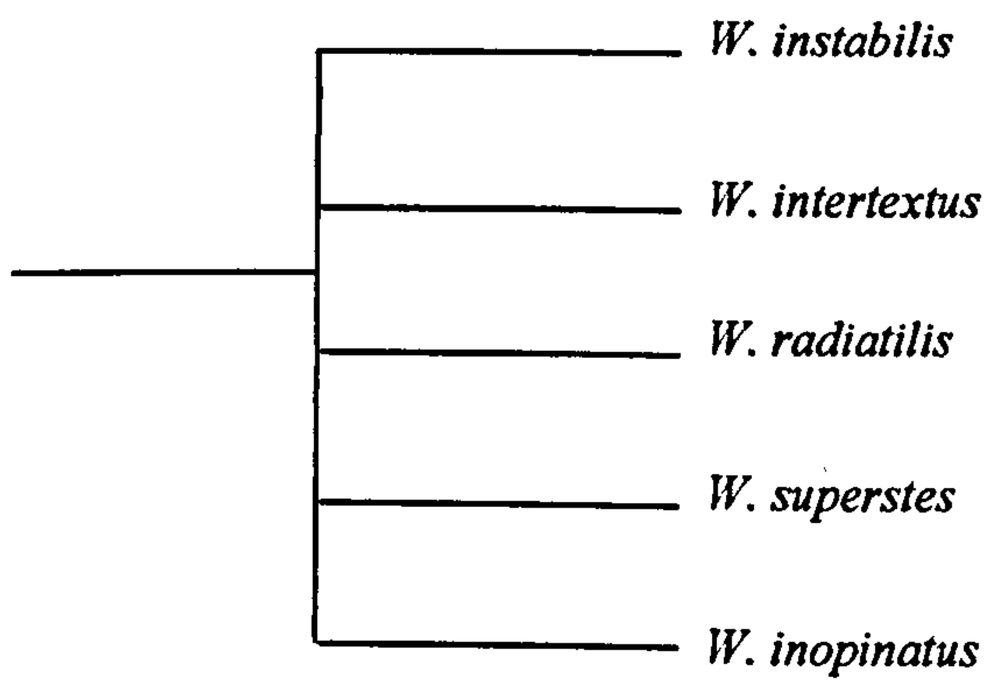
Range. Betton and Meadowtown Formations, Llanvirn Series, upper Abereiddian and Llandeilian stages, *murchisoni* and *teretiusculus* biozones. Shelve, Shropshire, England and Llanfawr Mudstones, Wales.

Emended diagnosis. Semi-circular cephalic outline. Weak preglabellar field. Girder prominent; first internal pseudogirder developed. No girder list; generally distinct pseudogirder list. Radial sulci variably developed frontally and anterolaterally on upper lamella; E_1 and I_1 arc pits larger than inner pits, I_2 present mesially, I_3 starts anterolaterally, I_n terminated by I_3 or I_4. Radial alignment to posterior area where pits small and irregularly distributed.

Remarks. Whittard (1958) described three closely related species from the Llanvirn of the Shelve area: *Cryptolithus radiatilis*, *C. intertextus* and *C. inopinatus*. Hughes (1971) erected *Cryptolithus instabilis* for specimens from the Builth/Llandrindod district of Powys, mid Wales, showing arcs I_4 and I_5 starting much further from the sagittal line. Hughes *et al.* (1975) designated this species as the type species for *Whittardolithus*. The presence of I_2 mesially, I_3 frontally and large area of irregular pits posteriorly are sufficient characters to retain *Whittardolithus* as a genus distinct from *Bettonolithus*. Hughes *et al.* (1975) and Bettley (unpublished thesis, 1998) highlighted *W. superstes* as being intermediate between *Bettonolithus* and *Whittardolithus*. Under the emended diagnosis *superstes* clearly belongs in *Whittardolithus* and is here considered to be the senior subjective synonym of the type species *W. radiatilis*. However, it does draw attention to the close affinities between the two genera.

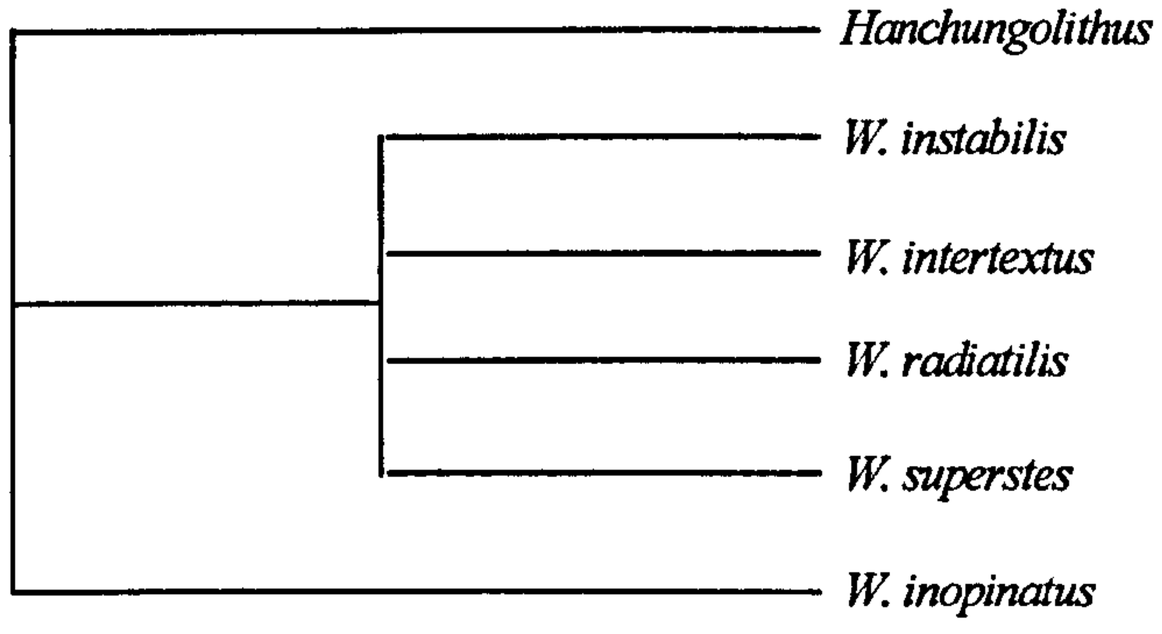
The previously named species of *Whittardolithus* show considerable morphological similarity and are all here considered to be synonyms.

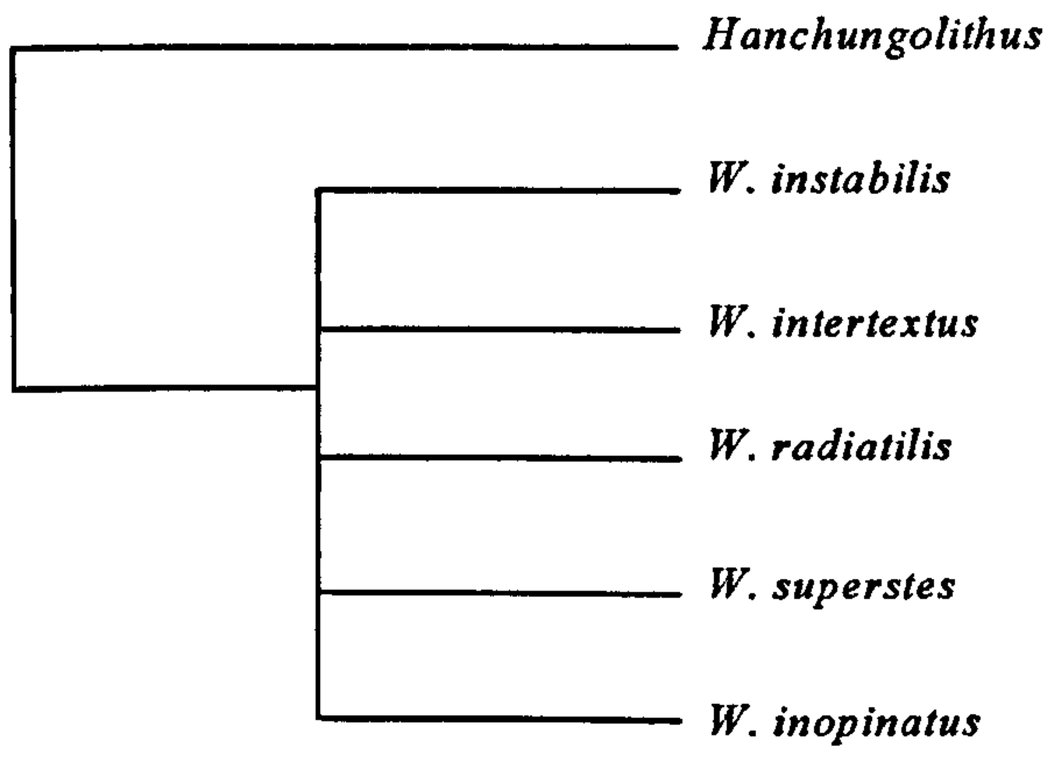
The cladistic analysis of all marrolithine species produced a discrete clade for *Whittardolithus* with its component "species" forming an unresolved polytomy, highlighting their close similarity (Text-fig. 4.12).



Text-fig. 4.12 . *Whittardolithus* subclade from the consensus tree resulting from the species level cladistic analysis of the Marrolithinae (see Text-fig. 3.24).

Cladistic analysis of *Whittardolithus* with the ancestral outgroup produced two trees (length 14, C. I. = 0.547) one with no subclades, again highlighting the remarkably close similarity of the "species". The other tree shows a separation of *W. inopinatus* on the basis of its I_3 arc extending mesially.





Text-fig. 4.13 Cladistic analysis of the "species" of *Whittardolithus* with *Hanchungolithus* as the ancestral outgroup. Both trees are of length 14, C. I. = 0.547.

Whittardolithus superstes (Whittard, 1958)

Plate 8, Figs 4-10, Text-Fig 4.12,13,14.

1956 *Bettonia superstes* Whittard; p. 70, pl. 9, figs 15.

1958 *Cryptolithus radiatilis* Whittard; p. 76, pl. 11, figs 1,2.

1958 *Cryptolithus intertextus* Whittard; p. 74, pl. 10, figs 8-11.

1958 *Cryptolithus inopinatus* Whittard; p. 72, pl. 10, figs 1-7.

1970 *Cryptolithus* cf. *inopinatus* Morris *in* Toghill, p. 122.

1970 *Cryptolithus intertextus* Whittard; Morris *in* Toghill, p. 122.

1971 *Cryptolithus instabilis* Hughes; p. 152, pl. 9, figs 4-6, 8; pl. 10, figs 1-8; pl. 11, figs 5, 12.

1971 *Cryptolithus* sp. A Hughes; p. 157, pl. 11, figs 1, 6.

1971 *Cryptolithus* sp. B Hughes; p. 157, pl. 11, figs 2, 7.

1971 *Cryptolithus* sp. C Hughes; p. 152, pl. 11, figs 3, 8.

1971 *Bettonia* aff. *superstes* Whittard; Hughes, p. 167, pl. 14, fig. 11.

1975 *Whittardolithus instabilis* (Whittard); Hughes *et al.*, p. 576, pl. 7, figs 84, 85.

1975 *Whittardolithus intertextus* (Whittard); Hughes *et al.*, p. 576.

1975 *Whittardolithus superstes* (Whittard); Hughes *et al.*, p. 576.

1975 *Whittardolithus radiatilis* (Whittard); Hughes *et al.*, p. 576.

1975 *Whittardolithus inopinatus* (Whittard); Hughes *et al.*, p. 576, pl. 7, fig. 83.

1987 *Whittardolithus*; Sheldon, pp.561-562, fig. 4.

1988 *Whittardolithus instabilis* (Whittard); Morris, p. 237.

1988 *Whittardolithus intertextus* (Whittard); Morris, p. 237.

1988 *Whittardolithus superstes* (Whittard); Morris, p. 238.

1988 *Whittardolithus radiatilis* (Whittard); Morris, p. 237.

1988 *Whittardolithus inopinatus* (Whittard); Morris, p. 237.

1988 *Whittardolithus*; Sheldon, figs 7, 11.

Holotype. Slightly deformed internal mould of near complete specimen. By original designation; BGS GSM 86799 from the Betton Formation, lower Llanvirn Series, upper Abereiddian Stage, upper *murchisoni* Biozone from a tributary of Lower Wood Brook, Meadowtown, Shelve, Shropshire, England.

Other material. About 300 specimens. Generally flattened by sediment compaction and distorted by sediment compaction (making pit counting difficult). Some complete individuals. The majority are cranidia, cephala and lower lamellae that are generally incomplete. Most specimens are between 8-24 mm wide across the cephalon.

Distribution. Betton Shale Formation, Llanvirn Series, upper Abereiddian Stage, upper *murchisoni* Biozone of bank in tributary of Lower Wood Brook, 265 m N of White House, Meadowtown; 73m south of well, Meadowtown – Castle Ring Lane, Shropshire. Topmost Meadowtown Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of quarry 275 m northeast of Betton Wood Farm; quarry southwest of Meadowtown; road section along Meadowtown – Rorrington Road; 200 m southwest of Church Middleton; Lane to Waitchley, 128 m north of Meadowtown Chapel; ploughed field south-southeast of Mincop, all from Shropshire. Lower Llanfawr Mudstone Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of stream bank in Dulas Brook, 138 m southwest of Maesgwyne; 146 m southeast of Trecoed; Wellfield Lodge, all from Builth district; Penddol Rocks, Builth Wells; Hendre Shale Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of Bluffs at north corner of Wood in Pant-yr-Hendre quarry, Meirdrim, S. Wales. (This species is found along with *Lloydolithus lloydi* in the top most Meadowtown Formation).

Diagnosis. Subrounded cephalic outline. E_1 and I_1 pits larger than other pits; radial alignment frontally; sulcate inner pits. I_2 present mesially; I_3 present frontally and anterolaterally in a few specimens; I_4 present frontally. I_2-I_4 and I_n sulcate frontally; In cut-off by I_3 or I_4. Small irregular pits posteriorly. Recorded counts: E_1, 24-32 (mean, 28); I_1, 24-30 (mean, 28); I_2, 25-30 (mean, 28).

Description. Cephalic outline subrounded; margin gently upturned frontally. Glabella narrow; preglabellar field. Glabellar node and three pairs of lateral furrows present. Genal lobes wider laterally than fringe. E_1, I_1, I_2 and I_n present mesially; I_3 begins frontally; I_n cut-off by I_3. Numerous small, irregularly placed pits posteriorly including F pits. E_1-I_1 radially aligned; I_1 to I_n frontally show radial alignment and are sulcate in some specimens. E_1 and I_1 arc pits larger than inner pits. Recorded counts: E_1, 24-32 (mean, 28); I_1, 24-30 (mean, 28); I_2, 25-30 (mean, 28), see Text-Fig. 4.14. Distinct first internal list. Posterior margin extension present; short genal prolongation. Girder prominent along whole fringe; first internal pseudogirder present along whole fringe. Occipital spine present. Six thoracic segments of typical trinucleid pattern. Pygidium strongly ribbed with 6-8 axial ribs.

Remarks. Whittard (1956) established the species *superstes* and placed it within *Bettonolithus* [then *Bettonia*] on the grounds of its adventitious pits frontally and posteriorly. Whittard described adventitious pits from the posterolateral areas of *superstes* as being a unique character. The holotype of *superstes* (BGS GSM 86791) shows closely packed E_1 pits posteriorly and this is probably what he meant by adventitious pits. This feature is common in the three new species Whittard (1958) described (*Cryptolithus radiatilis, C. intertextus, C. inopinatus*) all remarkably similar to *superstes*, all from the same area and, importantly, the same horizons, but he did not compare them to *superstes*. Whittard differentiated the three species mainly on the radial arrangement of the pits of the fringe being lost more anteriorly in *C. intertextus* than in *C. inopinatus* and finally *C. radiatilis* which shows arcs extending towards the posterior margin. However, on close inspection the small irregularly distributed pits cover almost the same fringe area. The range of pit counts for all arcs show considerable overlap (see Text-Fig. 4.14).

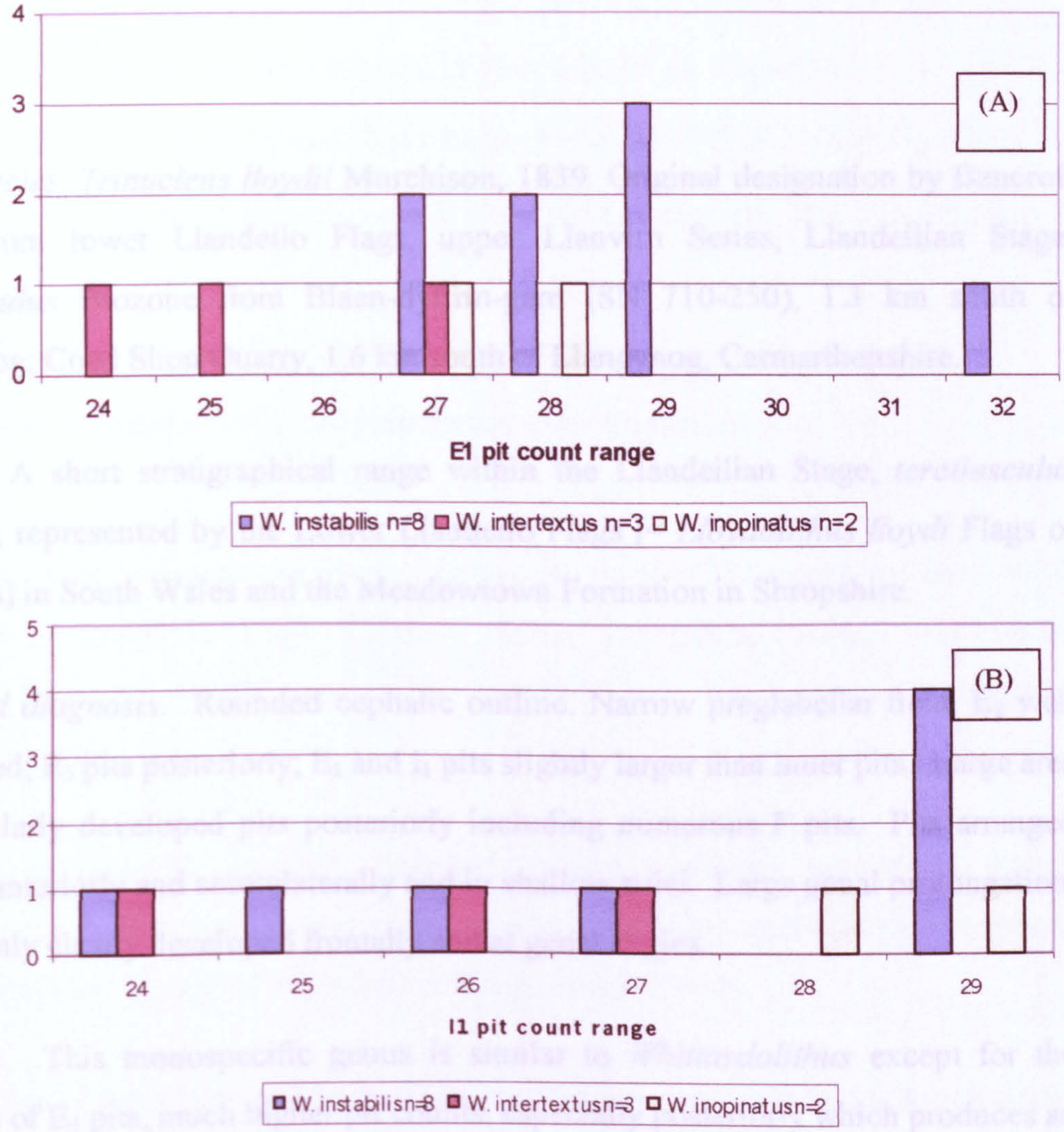
Hughes (1971, p. 156) distinguished *instabilis* from *inopinatus* on the basis of the more posterior start of arcs I_3 and I_4 in *instabilis*. This is quite clear in the type material from Maesgwynne at Builth, but other specimens which Hughes assigned to *instabilis* do not show this distinction. The differences in substrate have affected the quality of preservation in the two "species"; *Whittardolithus inopinatus* mainly from carbonates in the Meadowtown Formation is well preserved in an unflattened

condition whereas *W. superstes* from fine silt and mud substrates is less well preserved and has undergone some degree of flattening.

Although fragmentary, most specimens that Hughes (1971) termed *Cryptolithus* sp. A, B and C show characteristics of *Whittardolithus superstes*. However, a fragment of a pygidium (It. 2807) attributed to *Cryptolithus* sp. A, is not a marrolithine; pygidial interpleural furrow of marrolithines flex rearwards, Hughes' pygidium shows furrows curving forwards. Bettley (unpublished thesis 1998) suggested it may be an immature raphiophorid. The pygidium shows the curvature of the pleural ribs flex anteriorly near the margin whereas in the Marrolithinae the pleural ribs curve rearwards. An immature raphiophorid is the most plausible identification of the pygidium.

Sheldon (1987) studied the change in pygidial rib counts in Ordovician trilobites from the Builth district, including *Whittardolithus*. He found there was a gradual stratigraphical change up through the Lower Llanfawr Mudstone Formation, upper Llanvirn Series, Llandeilian Stage in the number of pygidial ribs seen in *Whittardolithus* from 5.5 to 6.5 and then a reversal to about six ribs. Whittard recorded about seven to eight pygidial ribs in *W. inopinatus*, *W. intertextus* and *W. radiatilis* and noted that the specimens (*W. inopinatus*) preserved in limestone showed the strongest definition of pygidial ribs. The present study has revealed a range of rib counts, between five and eight and particular "species" do not appear to be restricted to a single number of ribs. Sheldon (1987) remarked that the variation observed negates the usefulness of the feature as a diagnostic species character and he also suggested that the change was not ecophenotypic as the trend was not followed by other lineages at Builth. *Whittardolithus superstes* as designated herein shows variation in fringe pit counts and number of pygidial rib counts encompasing that of the taxa now included in its synonymy.

Přibyl and Vokm (1969) commented on the apparent similarity between *Whittardolithus* and *Cryptolithus abductus* [now *Onnia abductus*] in that both show a well-developed radial arrangement of pits. Higher numbers of arcs and pits and, significantly, the prominent girder in *Whittardolithus* differentiate this genus from specimens assigned to *Onnia abductus* which show lower arc and pit counts and only a weak girder but a prominent first internal pseudogirder.



Text-fig. 4.14. Histograms of *Whittardolithus* "species" showing the range of pit counts for arcs (A) E_1 and (B) I_1 from samples from the type localities of *W. instabilis*, *W. intertextus* and *W. inopinatus*. All are considered to be junior subjective synonyms of *W. superstes*.

Genus **LLOYDOLITHUS** Bancroft, 1933

Type species. Trinucleus lloydii Murchison, 1839. Original designation by Bancroft 1933, from lower Llandeilo Flags, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Blaen-dyffrin-garn (SN 710-250), 1.3 km south of Llangadog; Coed Shon Quarry, 1.6 km south of Llangynog, Carmarthenshire. .

Range. A short stratigraphical range within the Llandeilian Stage, *teretiusculus* Biozone, represented by the Lower Llandeilo Flags [= *Lloydolithus lloydi* Flags of Williams] in South Wales and the Meadowtown Formation in Shropshire.

Emended diagnosis. Rounded cephalic outline. Narrow preglabellar field. E_2 well developed; E_3 pits posteriorly; E_1 and I_1 pits slightly larger than inner pits. Large area of irregularly developed pits posteriorly including numerous F pits. Pits arranged radially anteriorly and anterolaterally and in shallow sulci. Large genal prolongation. Girder only clearly developed frontally and at genal angles.

Remarks. This monospecific genus is similar to *Whittardolithus* except for the presence of E_3 pits, much higher pit counts, especially posteriorly which produces an extended genal prolongation. *Lloydolithus* is stratigraphically younger than *Whittardolithus* and is found in similar areas. *Lloydolithus* and *Whittardolithus* are possibly from one lineage. The cladistic analysis shows them as sister groups.

Lloydolithus lloydi (Murchison, 1839)

Plate 8, Figs 1-3

1839 *Trinucleus Lloydii* Murchison, pp. 363, 650, pl. 23, fig. 4.

1853 *Trinucleus Lloydii* Murchison; Salter, dec. 7, p. 1 of pl. 7, figs 1, 3, 5.

1853 *Trinucleus Lloydii* var. *β Corndensis* Salter, p. 1 of pl. 7, figs 2, 6.

1933 *Lloydolithus lloydi* (Murchison); Bancroft, p. 2.

1941 *Lloydolithus lloydi* (Murchison); Whittington, p. 24, pl. 6, figs 24, 28.

1958 *Lloydolithus lloydi* (Murchison); Whittard, p. 79, pl. 11, figs 4-18.

1975 *Lloydolithus lloydi* (Murchison); Hughes et al., p. 577, pl. 7. figs 81, 82.

1981 *Lloydolithus lloydi* (Murchison); Wilcox and Lockley, pp. 299, 312, text-figs 2, 6, table 1.

1988 *Lloydolithus lloydi* (Murchison); Morris, p. 131.

see Whittard (1958) for full synonymy for the older literature.

Holotype. Near complete specimen of composite moulds. By monotypy; BGS 6839, from Lower Llandeilo Flags, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Blaen-dyffrin-garn (SN 710-250), 1.3 km south of Llangynog, Carmarthenshire.

Material. Around 70 generally flattened, poorly preserved specimens, mostly fragmentary cranidia, cephala and lower lamellae with a few near complete trilobites and rare pygidia. Recorded cephalic width between 9-20 mm.

Distribution. Lower Llandeilo Flags, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Blaen-dyffrin-garn (SN 710-250), 1.3km south of Llangynog; Coed Shon Quarry, 1.6km south of Llangadog, Carmarthenshire. Lower Llanfawr Mudstone Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of stream bank in Dulas Brook, 138 m southwest of Maesgwynne, Builth Wells, Wales. Meadowtown Formation, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Betton Quarry, Betton Wood Farm, Meadowtown; 686m south of Spy Wood Cottage; 200m west of Holy Trinity Church, Chirbury; Middleton, east of Chirbury; Dingle, northeast of Rorrington; road cutting between Meadowtown and Rorrington; coppice, 396m W40°N of bench mark 754, Little Weston, Shropshire. Hendre Shale Formation, Llanvirn Series, Llandeilian Stage 847m west of Ty-newydd Farm, Merthyr and Meidrim, Carmarthenshire.

Diagnosis. Rounded cephalic outline. Narrow preglabellar field. E_2 well developed; E_3 pits posteriorly; E_1 and I_1 pits slightly larger than inner pits. Large area of irregularly developed pits posteriorly including numerous F pits (which can only be identified on the lower lamella). Pits arranged radially anteriorly and anterolaterally and in shallow sulci. Large genal prolongation. Girder only clearly developed frontally and at genal angles. Recorded pit counts: E_2, 31-36 (mean, 34); E_1, 31-37 (35); I_1, 30.

Remarks. The holotype, collected by Murchison was considered by him to be from Blaen-dyffrin-garn, near Llangynog, Carmarthenshire, although the museum catalogue states Coed Sion quarries as the type locality. The poor preservation of most material does not allow for pit counting of more than a handful of specimens. Meraspids preserve the regular radial pattern over a much greater area of the fringe than larger individuals, as is also seen in *Whittardolithus*.

Well preserved pygidia of *Lloydolithus* show reticulation near the posterior margin. This is also seen in the new genus *Hammannaspis* (see above).

Lloydolithus lloydi inhabited a broad range of shelf environments. Wilcox and Lockley (1981) reported the species in beds within the siltier deposits deposited in near-shore shallow waters of the Llandeilo district, Wales. In South Wales *Lloydolithus* is found with Mar*rolithus favus favus* and in the Shelve area of Shropshire it occurs with *Whittardolithus superstes* in deeper water facies.

Genus **PROTOLLOYDOLITHUS** Williams, 1948

Type species. Trinucleus ramsayi Hicks, 1875. Original designation by Williams, (1948) from the Aber Mawr Shale Formation, Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone, Porth Llauog, Ramsey Island, Pembrokeshire, Wales.

Range. Llanvirn of Wales, Shropshire, Cambridgeshire (subsurface) and Portugal.

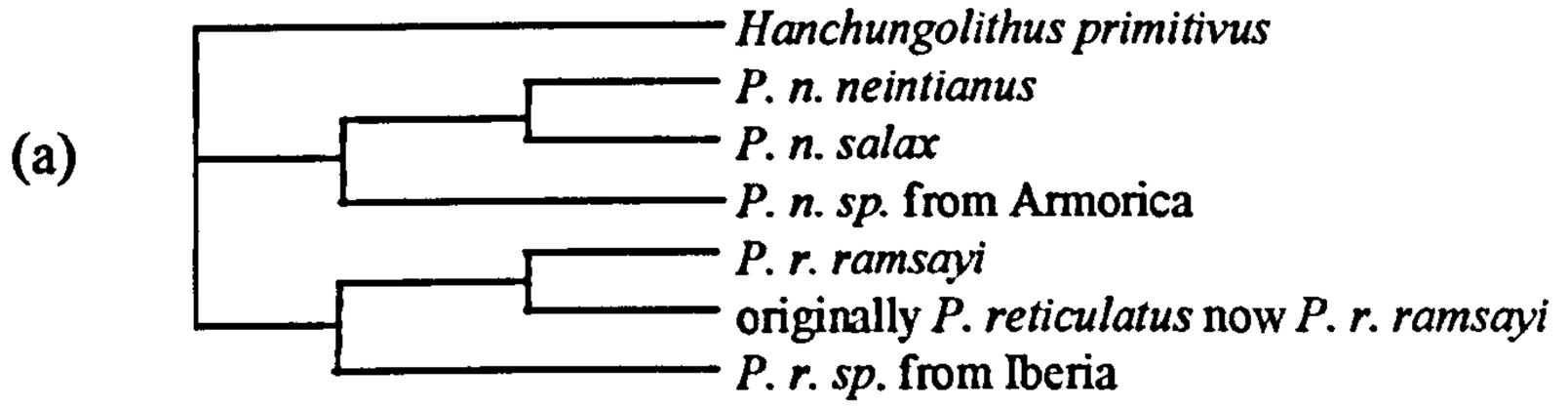
Emended diagnosis. Subrounded to subrectangular cephalic outline. E_1 pits larger than other pits. I_n clearly developed to posterolateral position; remainder of fringe consists of small pits with some irregular distribution. F pits developed (best seen on the lower lamella) around the genal lobe. Girder prominent; girder list sharp. No occipital spine.

Remarks. Protolloydolithus is the most primitive member of the Marrolithinae and was erected by Williams (1948) as a subgenus of *Lloydolithus* to include *Trinucleus ramsayi* Hicks, 1875 and *Trinucleoides reticulatus* Elles, 1940. Lu (1964) and later Dean (1966) showed that "*Trinucleus*" *primitivus* Born, 1921, placed in *Protolloydolithus* by Whittard (1956), should be transferred to *Hanchungolithus* Lu, 1954 on account of its marginal or submarginal girder. *Hanchungolithus* is the most likely ancestor for *Protolloydolithus* and was already in eastern Avalonia by the Arenig and only small morphological changes (development of E_1 arc, F pits and I_n cut off) would be needed to produce *Protolloydolithus*. *Protolloydolithus reticulatus* (Elles,1940) from the Lower Llanfawr Mudstones, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of the stream section east of Brach-y-graig; Llandrindod Wells, has remained separated from *P. ramsayi* by its younger age and occurrence at different locations in the Welsh Borderland. However, *P. reticulatus* is here considered to be synonymous with *P. ramsayi*. The appearance of *P. ramsayi* in the upper *artus* Biozone and again in the upper *murchisoni* to lower *teretiusculus* biozones appears to reflect the occurrence of particular water depths which may explain its disappearance for a time ifrom the Welsh Borders. *P. ramsayi* is here

considered to comprise two geographical subspecies; *P. ramsayi* from Avalonia and *P.*cf. *ramsayi* from Iberia. *P. neintianus* is here considered to comprise two geographical subspecies; *P. n. neintianus* and *P. n. salax* from Avalonia.

Henry *et al.* (1993) described a single deformed internal mould of cephalon. IGR 2635, from the Andouillé Formation, Llanvirn Series, *Placoparia tournemini* Biozone, les Monneries, Andouillé, Armorican Massif, France. This specimen shows a subrectangular cephalic outline with the fringe narrower mesially than laterally, E_1 and I_1 pits larger than inner pits (E_1 about 28 pits), sharp girder list and moderate genal prolongation (see Plate 9, Fig. 7). However, the good radial alignment of pits, lack of I_n cut off, no F pits and a posterior fossula present are more characteristic of an hanchungolithine and is here moved to the genus *Hanchungolithus*.

As is noted above the cladistic analysis of all Marrolithinae species produced over two hundred trees, however when the analysis was run with only the described *Protolloydolithus* "species" and the ancestral outgroup of *Hanchungolithus*, only two trees, of length 16 (C. I. = 0.376), were produced (see Text-Fig 4.15). Tree (a) below closely matches that of the consensus tree of all species. The two trees show the French specimen (considered here to be an hanchungolithine) and the Portuguese individual as sister groups to the Avalonian taxa. Both the French and Portuguese taxa are associated with fauna of the *Placoparia tournemini* Biozone, Llanvirn and are much younger than the Avalonian specimens.



Text-fig .4.15. Cladistic analysis results for the described *Protolloydolithus* taxa with *Hanchungolithus primitivus*, as the outgroup. Tree length, 16 and C. I., 0.376.

Both trees show the three *P. neintianus* subspecies plotting together. Similarly *P. ramsayi* and *P. reticulatus* plot together and are here considered synonymous. The Iberian taxon is mobile between the two sister clades on the cladograms. The fringe shape and size associate the Portuguese specimen with *P. ramsayi* (as in tree (A)), whilst the more ordered arrangment of pits associates it with the *P. neintianus* clade in tree (B). The former is here considered to reflect the likely affinity of the Iberian specimen which is here termed *P. ramsayi* subsp. nov.

Protolloydolithus ramsayi (Hicks, 1875)

Pl. 9, Figs 1, 2; Text-Fig. 4.15

1875 *Trinucleus ramsayi* Hicks, p.183, pl. 10, figs 1-2.

1891 *Trinucleus ramsayi* Woods; p. 152.

1930 *Trinucleus ramsayi* Pringle; p. 18.

1940 *Trinucleoides reticulatus* Elles; p. 427, pl. 29, figs 6-9.

1941 *"Trinucleoides" reticulatus* Elles; Lamont, p. 433.

1941 *Trinucleoides reticulatus* Elles; Whittington p. 26.

1948 *Lloydolithus* (*Protolloydolithus*) *ramsayi* (Hicks); Williams, p. 66, text-fig. 1.

1952 *Lloydolithus* (*Protolloydolithus*) *ramsayi* (Hicks); Whittington, p. 9.

1953 *Lloydolithus* (*Protolloydolithus*) *ramsayi* (Hicks); Williams, p. 179.

1956 *Protolloydolithus reticulatus* (Elles); Whittard, p. 41.

1971 *Protolloydolithus reticulatus* (Elles); Hughes, pp. 169-174, text-fig. 12, tables 36-38, pl. 15, figs 1, 5-9, 11; pl. 16, fig. 2.

1975 *Protolloydolithus ramsayi* (Hicks); Hughes *et al.*, p. 577.

1975 *Protolloydolithus reticulatus* (Elles); Hughes *et al.*, p. 577.

1988 *Protolloydolithus ramsayi* (Hicks); Morris, p. 191.

1988 *Protolloydolithus reticulatus* (Elles); Morris, p. 191.

1989 *Protolloydolithus ramsayi* (Hicks); Kennedy, p. 33, pl. 8, figs 1, 8, 11.

1989 *Protolloydolithus* sp.; Kennedy, p. 33, pl. 8, fig. 2.

Lectotype. Deformed partial dorsal exoskeleton of cephalon and thorax; fringe missing mesially and posteriorly. Selected by Morris (1988); BGS GSM 25401, original of Hicks 1875, pl. 10, fig. 1, from the Aber Mawr Shale Formation, Lower

Llanvirn Series, lower Abereiddian Stage, *artus* Biozone, Porth Llauog, Ramsey Island, Dyfed, Wales.

Other material. 58 specimens mainly distorted cephala, crandia and lower lamellae, and eight complete or near complete individuals.

Distribution. Upper *artus* Biozone of Llandeilo district, Wales and Shelve. Upper *murchisoni* and lower *teretiusculus* biozones of Southwest and Central Wales. Aber Mawr Shale Formation, Llanvirn, Abereiddian, *artus* Biozone of Porth Llauog, Ramsey Island; Porth Gain Quarry; St. Davids Pembrokeshire. Tuffs of the Stapeley Volcanic Member, Hope Shale Formation, Lower Llanvirn Series, lower Abereiddian Stage, upper *artus* Biozone of spoil heap from trial level, Whitsburn Dingle, Shropshire. Hope Shale Formation, Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone of Leigh Lane, Brookless Coppice, Leigh, Shropshire. Lower Llanfawr Mudstones, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of stream section east of Brach-y-graig; Llandrindod Wells. "*bifidus* Shales", Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone of stream section 305 m southwest of Pen-lan Farm; 110 m west of bridge at Lan Mill, Lampeter Velfrey, Pembrokeshire, Wales. Llanfallteg Formation, Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone immediately behind Cefn-mean-llŵyd farmhouse at Rhyd-y-wrâch, Whitland, Wales. Ffairfâch Group, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of 450 m ENE of Cwm Breinant, Llandeilo, Carmarthenshire, Wales.

Diagnosis. Subrounded cephalic outline. E_1 well defined, pits larger than inner pits; I_1 well developed. Girder and girder list well developed. Fringe same width mesially to posterolaterally. Slight radial alignment of inner pits frontally. Preglabellar field. Moderate genal prolongations. No occipital spine. E_1 about 20-30 pits.

Remarks. Williams (1948) separated *ramsayi* from *Dionide atra* Salter after Reed (1912) had synonymised them. Salter's species is correctly placed in *Dionide* (eg. see Morris, 1988, p. 80). Williams based a comprehensive redescription of the species based primarily on one specimen. Hughes (1971) described new material of *P. reticulatus* from Central Wales and stated that it differed from *P. ramsayi* in its larger

genal prolongations, better developed alae, fewer I arcs and narrower pygidium. However, these supposed differences between *P. ramsayi* and *P. reticulatus* are due to deformation during and post-burial (both sediment compaction and tectonic activity). Alae development, genal prologation, mesial fringe width and pygidium width are very variable within specimens ascribed to *P. reticulatus*. As well as supposed morphological differences, *P. reticulatus* has hitherto been retained as separate from *P. ramsayi* on geographical and stratigraphical grounds. *P. ramsayi* occurs in the upper *artus* Biozone of southwest Wales whilst *P. reticulatus* was described from beds of the upper *murchisoni* and lower *teretiusculus* biozones of Central Wales and Shropshire. These two intervals represent periods of approximately equal water depths associated with the Llanvim transgression in eastern Avalonia. The cladistic analysis (Text-Fig. 4.15) shows no difference between the two "species" and *P. reticulatus* is here synonymised within *P. ramsayi*, thus increasing the range of the nominate species.

Protolloydolithus cf. *ramsayi* (Hicks, 1875)

Pl. 9, Figs 5; Text-fig. 4.15

1990 *Protolloydolithus* sp. Romano; pp. 487-493, text-figs 2-3.

Occurrence. A single distorted internal mould of nearly complete upper lamella and external mould of part of lower lamella, PGS SG 6717, from the Valongo Formation, Llanvirn, *Placoparia tournemini* Biozone of Covelo, Valongo, Portugal.

Description. The specimen shows a stress fracture in line with the left axial furrow. The left side of the fringe has not been affected by deformation to the same extent as the right half. Cephalic outline semicircular. Fringe flat and of constant width around cephalon. E_1 arc raised. E_1 pits larger than all other pits. E_1 approximately 30 pits

(mid-line difficult to determine). I_1 arc clearly visible. I_n arc clearly visible, cut-off posteriorly by internal pits (arc number difficult to determine). Pits of arcs close to I_n show good radial alignment, puckering of the fringe near the stress fracture suggests alignment of pits extending outwards towards I_1 arc.

Remarks. This specimen closely resembles *P. ramsayi* but its position varies between the two *Protolloydolithus* cladograms (Text-fig. 4.15). It is regarded here as *P.* cf. *ramsayi* as some degree of uncertainty is present in its cladogram position.

Protolloydolithus neintianus neintianus Whittard, 1956

Plate 9, Figs 3; Text-figs 4.15, 16.

1956 *Protolloydolithus neintianus* Whittard; p. 42, pl. 5, figs 13-15; pl. 6, figs 1-3.

1975 *Protolloydolithus neintianus* Whittard; Hughes *et al.*, p. 577, text-fig. 3, pl. 6, figs 79, 80.

1988 *Protolloydolithus neintianus* Whittard; Morris, p. 191.

2001 *Protolloydolithus* sp.; Bettley *et al.*, fig. 6.

Holotype. Complete dorsal exoskeleton. By original designation; BGS GSM 92984, from the Stapeley Volcanic Member of the Hope Shale Formation, lower Llanvirn Series, lower Abereiddian Stage, upper *artus* Biozone of Nind Quarry, Shelve, Shropshire, England.

Other material. A few (less than 10) well preserved internal moulds and original exoskeletons of cephala (between 4-18 mm wide) and lower lamellae. Less than 30 fragments of external moulds.

Distribution. Tuffs of the Stapeley Volcanic Member of the Hope Shale Formation, lower Llanvirn Series, lower Abereiddian Stage, upper *artus* Biozone of Whitsburn Dingle; Tasgar and Nind quarries; 248 m NNW of entrance to Linley Drive, Shelve, Shropshire. Hope Shale Formation, Llanvirn, Abereiddian, *artus* Biozone of Stream section, Pentrivin, Shropshire.

Diagnosis. Subrectangular cephalic outline; fringe narrower frontally than laterally. E_1 and I_1 pits larger than other pits. Radial alignment of pit mesially. Girder and girder list sharp. Shallow genal prolongations. No occipital spine. E_1, about 26-30 pits.

Description. Cephalon subrectangular in outline; fringe narrower frontally than laterally. Glabella narrow, elongate; glabellar node and three pairs of lateral furrows present. Genal lobes broader than fringe, lobes terminate in front of glabella in preglabellar field (especially in adults). E_1 pits large, E_1 arc raised with strong girder list. I_1 arc pits well defined and larger than inner pits. Inner pits irregularly distributed. I_n cut-off posteriorly. No genal prolongation. Girder strong, prominent ridge to genal spines. No occipital spine.

Remarks. *Protolloydolithus neintianus neintianus* co-existed with *P. ramsayi ramsayi* in the finer grained sediments of the Stapeley Volcanic Member in Whitsburn Dingle but are easily distingushed by the "kneeling-mat" shaped cephalic outline of the former.

Protolloydolithus neintianus salax Rushton and Hughes, 1981

Pl. 9, Figs 4, 6; Text-figs 4.15, 16.

1981 *Protolloydolithus salax* Rushton and Hughes, p. 631, pl. 3, figs 1-6, 8-10, 13.

1988 *Protolloydolithus salax* Rushton and Hughes; Morris. p. 191.

Holotype. Nearly complete specimen. By original designation; BGS By 8522, probably from the *artus* Biozone, Llanvirn Series of the Great Paxton Borehole, 8 km SW of Huntingdon, Cambridgeshire, England.

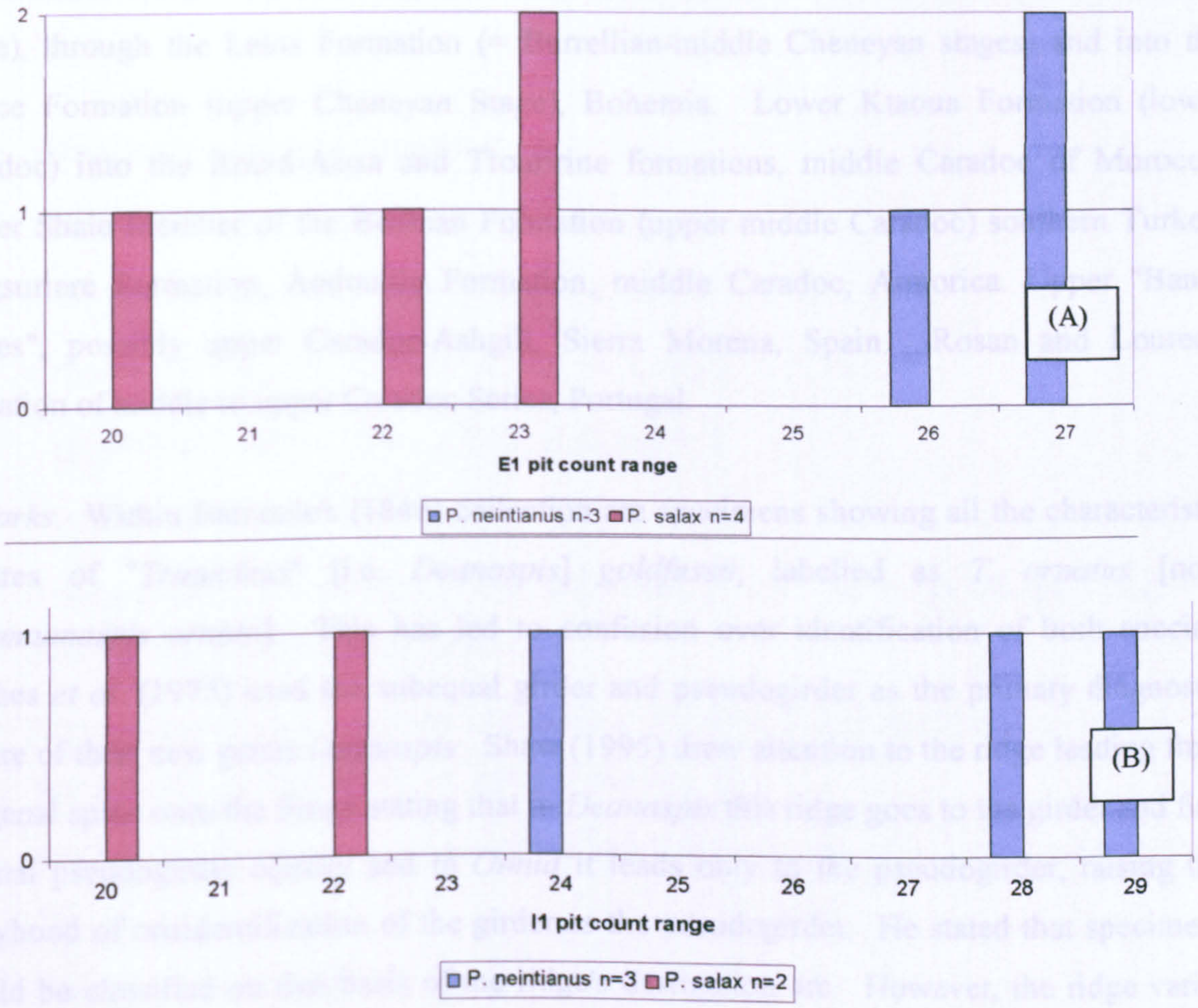
Other material. About 130 well preserved specimens of cranidia, cephala and lower lamellae and 16 complete individuals, eight of them enrolled.

Distribution. Probably from the *artus* Biozone, lower Llanvirn Series of the Great Paxton Borehole, 8 km SW of Huntingdon, Cambridgeshire, England.

Diagnosis. Distinct subrectangular cephalic outline strongly concave mesially. No preglabellar field. E_1 arc raised; E_1 and I_1 pits large; low pit counts E_1, about 20 to 23; I_1, 19-24; good radial alignment of inner arc pits mesially; slight ordering into arcs laterally. Girder and girder list sharp. No occiptial spine. Short genal prolongation.

Remarks. P. n. salax is closely related to *P. n. neintianus* in that they both show the development of well ordered E_1 and I_1 arcs, development of F pits and in overall morphology of the glabella and pygidium. The slightly lower pit counts (see Text-Fig. 4.16) and the distinctive cephalic of outline are sufficient to distinguish the Great Paxton specimens at subspecific level. Rushton and Hughes (1981) suggested that the distinct cephalic outline may be a preservational effect reflecting the development of a strong anterior arch. This is probably not the case as such flattening would result in stress fractures and these are rare in these individuals. Juvenile *P. n. neintianus*

specimens possess characters very similar to *P. n. salax* such as radial alignment of inner pits mesially, the distinctive cephalic outline and lack of preglabellar field (see Pl. 9, Figs 3 and 6). These characters are absent or indistinct in adults of *P. n. neintianus* and may indicate *salax* is ancestral to *neintianus*. That may suggest that *P. n. salax* is from the lower *artus* Biozone but the exact age of the horizon is presently undetermined.



Text-Fig. 4.16. Histograms showing (A) E_1 pit radius number and (B) I_1 pit radius number for type locality material for *Protolloydolithus n. neiantianus* and *P. n. salax*

Genus **DEANASPIS** Hughes, Ingham and Addison, 1975

Type species. Cryptolithus bedinanensis Dean, 1967. Bedinan Formation, upper middle Caradoc from south of Bedinan between Derik and Mardin, southeast Turkey. [= *D. goldfussii* (Barrande, 1846) herein]

Emended diagnosis. Fringe subsemicircular. E_1 pits small close; I_1 and I_2 arc pits larger than others. Distinct girder list and two internal pseudogirder lists posteriorly. Girder and first internal pseudogirder of subequal strength and distinct throughout.

Distribution. From the Řevnice Quartzite at the base of the Libeň Formation (= Aurelucian Stage), through the Letná Formation (= Burrellian-middle Cheneyan stages) and into the Vinice Formation (upper Cheneyan Stage), Bohemia. Lower Ktaoua Formation (lower Caradoc) into the Rouid-Aissa and Tiouririne formations, middle Caradoc of Morocco. Lower Shale Member of the Bedinan Formation (upper middle Caradoc) southern Turkey. Sangsuriere Formation, Andouille Formation, middle Caradoc, Armorica. Upper "Bancs mixtes", possibly upper Caradoc-Ashgill, Sierra Morena, Spain. Rosan and Louredo formation of middle to upper Caradoc Series, Portugal.

Remarks. Within Barrande's (1846) collection are specimens showing all the characteristic features of "*Trinucleus*" [i.e. *Deanaspis*] *goldfussii*, labelled as *T. ornatus* [now *Hammannaspis ornata*]. This has led to confusion over identification of both species. Hughes *et al.* (1975) used the subequal girder and pseudogirder as the primary diagnostic feature of their new genus *Deanaspis*. Shaw (1995) drew attention to the ridge leading from the genal spine onto the fringe stating that in *Deanaspis* this ridge goes to the girder and first internal pseudogirder equally and in *Onnia* it leads only to the pseudogirder, raising the likelyhood of misidentification of the girder as the pseudogirder. He stated that specimens should be classified on that basis of the ridge's destination arc. However, the ridge varies within species and is affected by taphonomic flattening and so should not be used as a diagnostic character. The presence of a continuous girder and a subequal first internal pseudogirder frontally remain the major diagnostic characters of *Deanaspis*. The Prague Basin has been the most studied area yielding *Deanaspis*. New material from Morocco shows an early form of *Deanaspis* that coexisted with the earliest known *Onnia*, indicating the previously thought linear relationship is not correct. The substantial synonymy of *Onnia* and

Deanaspis speices with *D. pongerardi* has produced a much clearer picture of the peri-Gondwanan distribution of the marrolithines and will aid in their corellation usefulness. Herein it is recognised that *Deanaspis* contains three species ranging through the Caradoc from Bohemia, Turkey, the Iberian and Armorican peninsulas, Sardinia and Uzebekistan.

Deanaspis goldfussii goldfussii (Barrande, 1846)

Pl. 10, Figs 1-8.

1846 *Trinucleus Goldfussii* Barrande; p. 31.

1847 *Trinucleus Senftenbergii* Hawle and Corda; p. 156.

1967 *Marrolitoides laticirrus* Dean, p. 99, pl. 2, figs 1, 3, 5, 11, 13, 14.

1967 *Cryptolithus* ? cf. *inferus* Dean, p. 102, pl. 2, figs 2, 4, 7, 12.

1967 *Cryptolithus* ? *inferus* Dean, p. 102, pl. 2, figs 6, 8.

1967 *Cryptolithus* sp. Dean, p. 107, pl. 2, figs 10.

1969 *Onnia goldfussi* (Barrande); Přibyl and Vaněk, p. 108., pl. 7, figs 1-6, pl. 8, figs 1-7, text-fig. 10; and references therein.

1969 *Marrolithus ornatus senftenbergi* (Hawle and Corda); Přibyl and Vaněk, p. 117, pl. 12, figs 1-9, pl. 13, figs 1-8, pl. 14, figs 1-9, text-fig. 13.

1969 *Marrolithus ornatus parviporus* Přibyl and Vaněk; p. 120, pl. 14, figs 10-14, text-fig. 14.

1972 *Onnia goldfussi* (Barrande); Čech, p. 245.

1975 *Onnia goldfussi* (Barrande); Čech, pp. 173-176.

1975 *Marrolithus? senftenbergi* (Hawle and Corda); Čech, pp. 175, pl. 1, figs 1-3, 5, 6, text-fig. 2

1975 *Onnia goldfussi* (Barrande); Čech pl. 3, figs 5-7.

1975 *Deanaspis goldfussi* (Barrande); Hughes *et al.* p. 573

1975 *Deanaspis bedinanensis* (Dean); Hughes *et al.* p. 573, pl. 9, figs 100,101.

1975 *Deanaspis senftenbergi* (Hawle and Corda); Hughes *et al.* p. 573.

1975 *Deanaspis parviporus* (Přibyl and Vaněk); Hughes *et al.* p. 574.

1981 *Deanaspis linol* Šnajdr; pl. 2, fig, 8.

1987 *Deanaspis goldfussi* (Barrande); Šnajdr, p. 284.

1990 *Deanaspis goldfussi* (Barrande); Šnajdr, p. 186.

1991 ?*Deanaspis* sp. Leone *et al*; pl. 2, fig. 1.

1995 *Deanaspis goldfussi* (Barrande); Shaw, pp. 13-17, pl. 13, figs 1-14; pl. 14, 1-5, 7, 8, 12.

1995 *Marrolithus ornatus* (Sternberg); Shaw (pars), pp. 11-13, pl. 11, fig. 5.

2001 *Deanaspis goldfussi* (Barrande); Vanek, p. 42.

2001 *Deanaspis parviporus* (Barrande); Vanek, p. 42.

2001 *Deanaspis senftenberi* (Barrande); Vanek, p. 42.

Lectotype. Internal mould of cephalon with external mould of lower lamella (upper lamella missing); selected by Přibyl and Vaněk (1969) NM L15197 (original number CD 699) original of Barrande (1852, pl. 30. figs 34a, 35). from the sandstones of the Letná Formation, Middle Caradoc Series, Burrellian-mid Cheneyan stages from Veselá, Prague Basin, Czech Republic.

Distribution. From the Řevnice Quartzite at the base of the Libeň Formation, Aurelucian, through the Letná Formation, middle Caradoc Series, Burrellian-mid Cheneyan stages and into the Vinice Formation, Caradoc Series, upper Cheneyan Stage, Bohemia. Lower Ktaoua Formation, lower Caradoc Series, Aurelucian Stage into the Rouid-Aissa and Tiouririne Formations, upper Caradoc Series, Streffordian Stage of Morocco. Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, upper Burrellian to lower Cheneyan stages of southern Turkey.

Diagnosis. E_1 arc pits small and closely packed; I_1 arc pits larger than rest, and often elevated slightly laterally; I_2 not present mesially; I_3 starts two to three pits posteriorly to I_2 start; I_n terminated by I_3 to I_5. Small area of irregular pits posteriorly. recorded ranges E_1, 25-38

(mean, 31); I_1, 18-31 (23.5); I_2, 15-26 (22) starting R0-R6 (R3); I_3, 11-27 (18) starting R3-R10 (R5.5); I_4, 4-22 (13); I_n, 11-24(17.5) terminated by arc 3-5 (4).

Description. Subsemicircular cephalic outline. Clavate glabella, generally with only one pair of lateral furrows and shallow occipital pits. Occipital ring narrow (sag.) tapering sharply into short occipital spine. E_1 arc pits small and closely packed particularly posterolaterally. I_1 pits are large over entire fringe, slightly raised posterolaterally in many specimens; I_2 and in some specimens, I_3 pits become larger laterally and posteriorly. I_2 extremely rare mesially (two specimens from over one hundred). In terminated by I4, or more rarely by I_3 or I_5. Moderate number of F pits and irregular positioned pits posteriorly (low twenties). Sharp girder list and two or three internal pseudogirder lists. Girder and first internal pseudogirder prominant throughout

Remarks. Shaw (1995) synonymised five taxa with *D. goldfussii goldfussii*, with the exception of ?*Deanaspis* sp. of Leone *et al.* (1991) these synonymies are supported here. Hammann and Leone (1997) established *D. g. fluminensis* for the latter material (see below). The numerous "species" from Bohemia were based on slight differences in cephalic outline, fringe structure and small variations in pit counts. Text-Fig. 4.17 shows the mean and range charts for half pit counts for the individual the "species" now synonymized within *D. g. goldfussii*. Each character shows an overlap in variation between there supposed species. The synonymy suggests that *Deanaspis goldfussii* was a geographically widespread, morphologically variable and stratigraphically long lived (~ 8 M. y., Havlíček and Marek, 1973, Shaw 1995) species. *D. senftenbergii* was based on numerous specimens from various localities in the lower Vinice Fm, upper-middle Caradoc. The fringe in dorsal view appears wide but nearly all specimens show taphonomic crushing. Shaw (1995) reported specimens that had previously been ascribed to *D. senftenbergii* from the Venice Fm showing alae, eye ridges and eye spots well developed in meraspis degrees 0-3. Degree 0 shows no fringe pits. Degree 1 has 1 then 2 arcs, outer arc with ~ 20 pits. Degree 2 shows 4 arcs. Degree 3 is essentially adult in pit pattern

D. bedinanensis from the Bedinan Formation, Caradoc, of Turkey is very similar to, the contemporaneous, *D. goldfussii*, differing only in having a few extra pits in the outer two arcs (3-5 pits more). It is here considered to be a junior subjective synonym of Barrande's species. *D. laticirrus* (Dean) and *D. inferus* (Dean) also from Turkey appears to have a slightly lower

pit count, but nonetheless within the range for *D. goldfussii goldfussii* (see Text-Fig. 4.17). *Deanaspis* is also known from Morocco (Hughes *et al.* 1975, Destombes *et al.* 1985a) but hitherto has remained undescribed. The Moroccan representatives show the same features as the Bohemian specimens and are contemporaneous with it. The pit counts are also similar: E_1, for *D. g. goldfussii*, 25-32 (29) n=7; for Moroccan material, 25-30 (27.5) n=12; I_n, 16-17 (16) n=4 cf. 11-17 (15) n=9; I_n cut off by arc I_4-I_5 (I_4) n=12 cf. I_4-I_5 (I_4) n=13; I_1, 23-24 (23.5) n=7 cf. 20-26 (23) n=13; I_2, 19-24 (22) n=6 cf. 18-24 (21) n=12. The only difference appears to be that the I_2 arc varies in its beginning position in Moroccan specimens from being complete frontally to lacking upto 5 pits frontally. This is not regarded as sufficient reason to keep the North African specimens separate from *D. g. goldfussii*.

Deanaspis goldfussii fluminensis Hammann & Leone, 1997

1975 *Deanaspis* sp. Hughes, Ingham and Addison; pp. 573-574, pl. 9, figs 102,103.

1991 ? *Deanaspis* sp. Leone *et al.*, pl. 2, figs 1, 4.

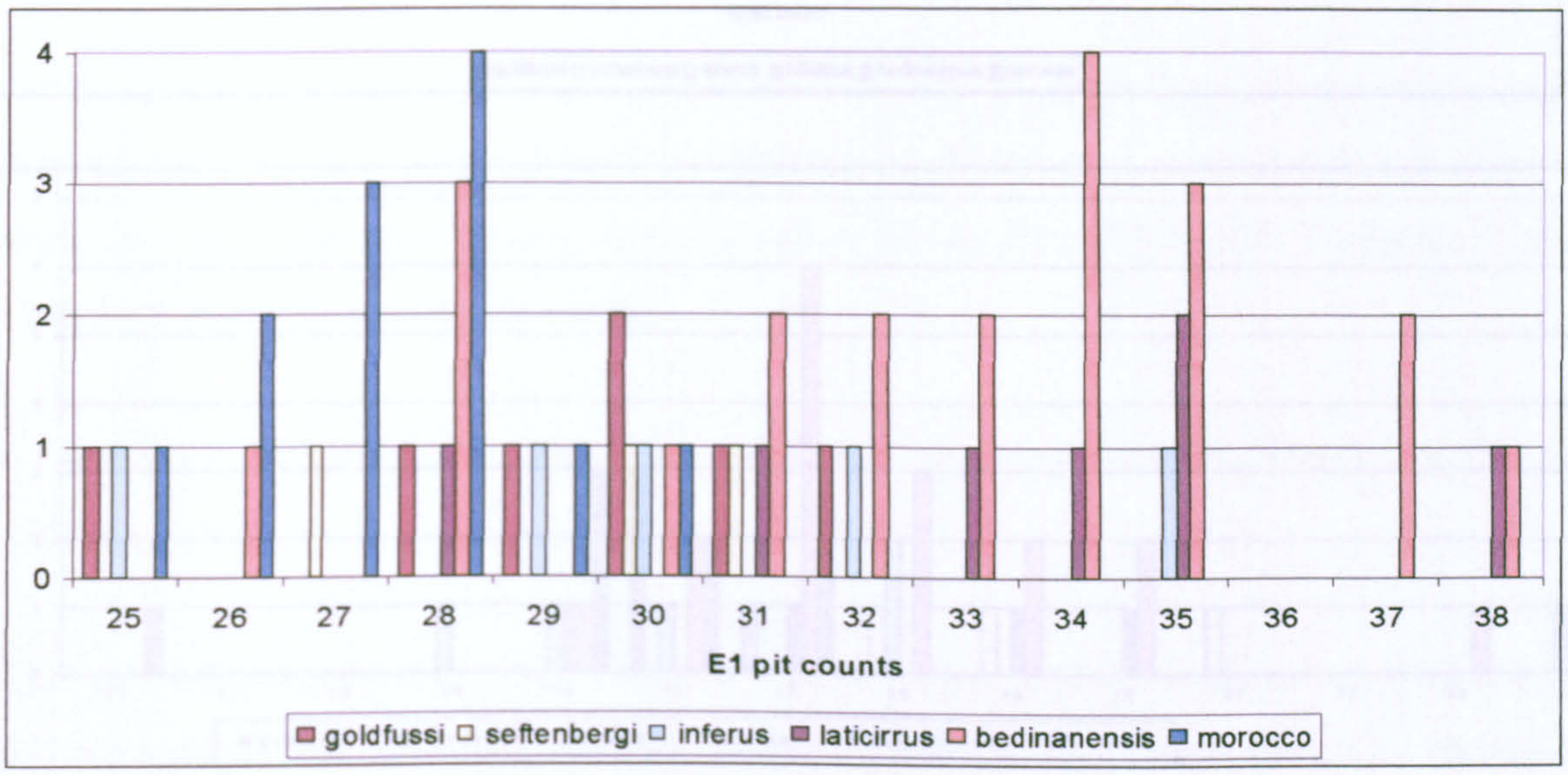
1997 *Deanaspis goldfussii fluminensis* Hammann and Leone; pp. 62-65, pl.25, figs 1-12.

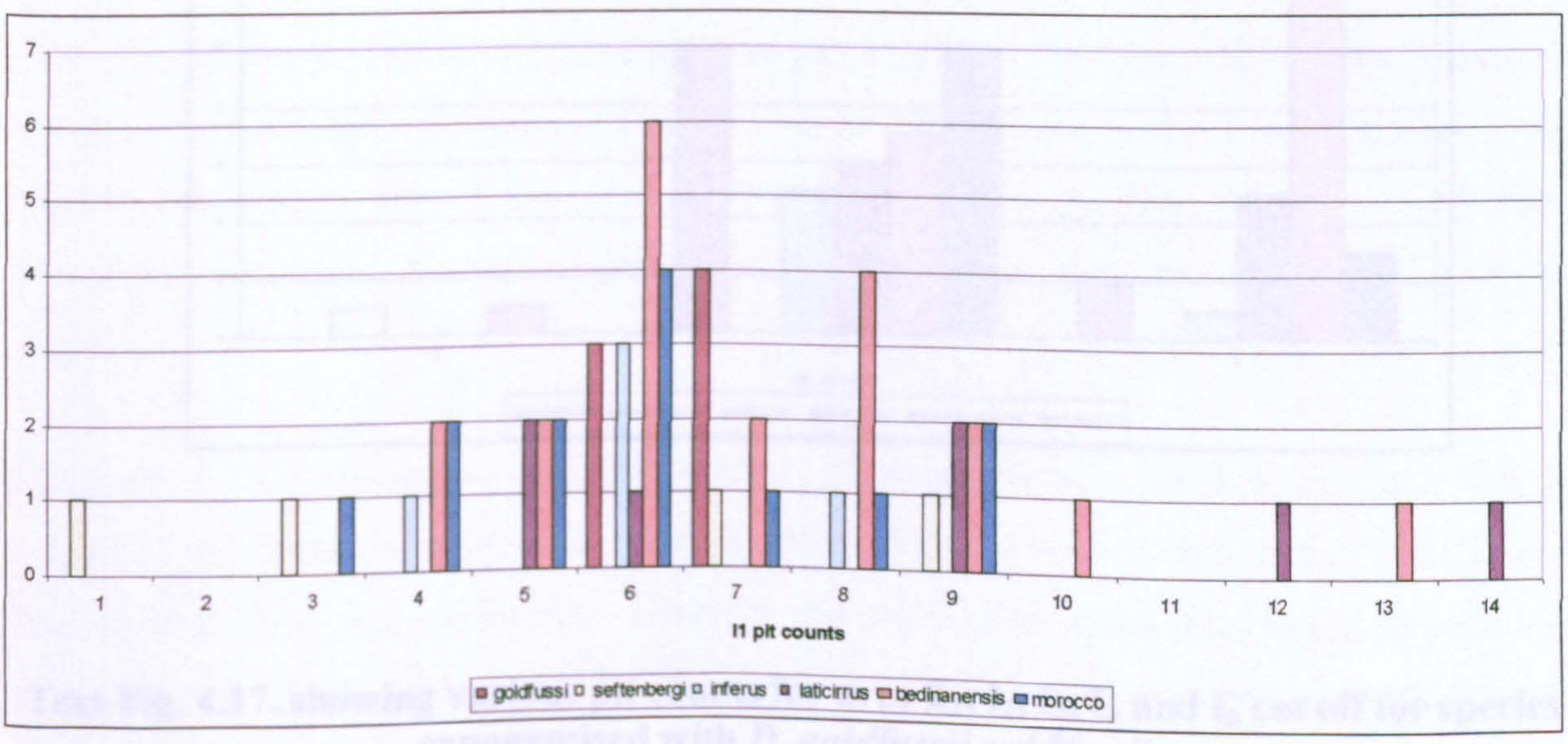
Holotype. A near complete cephalon showing internal and external moulds of fringe. by original designation; IPUM 52105. From the Monte Orri Formation, probably upper Caradoc Series, (Trilobite location TH1b of Hammann and Leone 1997), Via Pinna sole at Fluminimaggiore, southern Sardinia.

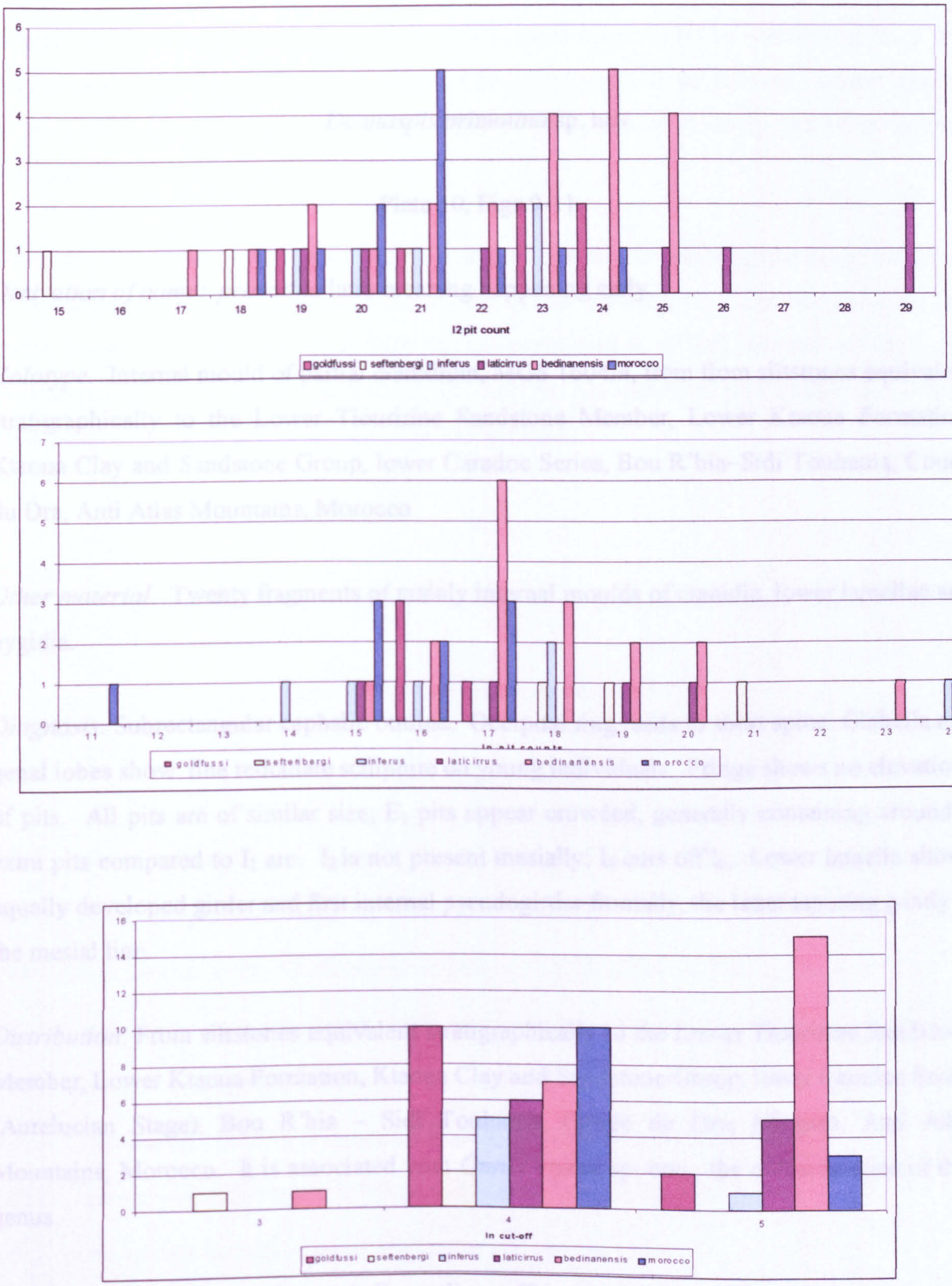
Distribution. The Monte Orri Formation and Portixeddu Formation, Upper Caradoc to lower Ashgill, southern Sardinia.

Diagnosis. I_1 arc pits larger than other pits on upper lamella; I_2 arc present mesially, pits becoming large posteriorly; I_n terminated by I_4 arc; E_1 arc tilted downwards laterally to posterior; sharp girder list. E_1 24-28 (25); I_1, 21-23; I_2, 21-23; I_3 about 19, starting at R3 or R4; I_4, 11-12, starting at R9-12; I_n, about 17, terminated by I_4.

Remarks. *Deanaspis goldfussii fluminensis* differs from *D. goldfussii goldfussii* by the downward tilt of the E_1 arc and I_2 present frontally, lower pit counts and generally one less inner arc (I_n cut off by I_3 or I_4 cf. I_4-I_5 in *D. g. goldfussii*). The specimen from Uzebekistan left under open nomenclature by Hughes *et al.* (1975) has been placed within *D. g. fluminensis* as they are remarkably similar in all respects.







Text-Fig. 4.17. showing various pit counts for arcs E_1, I_1, I_2, I_n and I_n cut off for species synonymised with *D. goldfussii goldfussii*.

Deanaspis primotina sp. nov.

Plate 10, Figs 9-11.

Derivation of name: primotina latin meaning happening early.

Holotype. Internal mould of partial cranidium, MGS 1604/4, from from siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series, Bou R'bia–Sidi Touhama, Coude du Dra, Anti Atlas Mountains, Morocco

Other material. Twenty fragments of mainly internal moulds of cranidia, lower lamellae and pygidia.

Diagnosis. Subrectangular cephalic outline. Occipital ring leads to short spine. Glabella and genal lobes show fine reticulate sculpture on young individuals. Fringe shows no elevations of pits. All pits are of similar size; E_1 pits appear crowded, generally containing around 8 extra pits compared to I_1 arc. I_2 is not present mesially; I_4 cuts off I_n. Lower lamella shows equally developed girder and first internal pseudogirder frontally, the latter tapering gently at the mesial line.

Distribution. From siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series (Aurelucian Stage), Bou R'bia – Sidi Touhama, Coude du Dra; Mizgarn, Anti Atlas Mountains, Morocco. It is associated with *Onnia etyma* sp. nov., the oldest species of that genus.

Description. Subrectangular cephalic outline. Clavate glabella, shallow occipital furrow, occipital ring leads to short spine. Genal lobes slightly swollen with broad axial furrow leading to shallow anterior fossula. Glabella and genal lobes show fine reticulate sculpture on young individuals. Fringe shows no elevations of pits. All pits are of similar size, but E_1 and I_1 often show slight size increase compared to other arcs. E_1 pits appear crowded, generally containing around 8 extra pits compared to I_1 arc.I_2 is not present mesially, starting

around row 4 or 5. I_3 present from row 5 or 6. I_4 starts around row 14 and cuts off I_n. F pits only present around genal lobe with only a few irregular pits posteriorly. Lower lamella shows equally developed girder and first internal pseudogirder frontally, the latter tapering gently at the mesial line.

Remarks. The distinct subequal girder and first internal pseudogirder and fringe pit arrangement leaves no doubt that these specimens are *Deanaspis*. The simple upper and lower fringe features possibly reflect the ancestral nature of this species to the other *Deanaspis* taxa. *Deanaspis primotina* sp. nov. is the oldest of this genus and is also associated with *Onnia etyma* sp. nov., the oldest *Onnia*.

Deanaspis pongerardi (Rouault, 1847)

Plate10, Figs 12, 14.

1847 *Trinucleus pongerardi* Rouault, pp. 312-315, pl. 3, figs 1, 1a, 1b.

1894 *Trinucleus grenieri* Bergeron, p. 45, pl. 6, figs 5,6.

1895 *Trinucleus pongerardi* Rouault; Oehlert, p. 306, pl. 2, figs 25-32.

1895 *Trinucleus grenieri* Bergeron; Oehlert, p. 306, pl. 2, fig. 33.

1900 *Trinucleus seunesi* Kerforne, p. 782.

1966 *Cryptolithus grenieri* (Bergeron); Coates, pp. 84-87, text-figs 4, 5 a-e.

1969 *Onnia grenieri* (Bergeron); Přibyl and Vaněk, pl. 16, figs 3-5.

1975 *Onnia pongerardi* (Rouault); Hughes *et al.*, pp. 574, 575.

1975 *Onnia grenieri* (Bergeron); Hughes *et al.*, pp. 574, 575.

1975 *Onnia seunesi* (Kerforne); Hughes *et al.*, pp. 574, 575.

1976 *Onnia* ? n. sp. aff. *grenieri* (Bergeron); Hammann, pp. 40-47, text-figs 2, 3, table 2, pl. 1, figs 1-10; pl. 2, figs 11-14.

1980 *Onnia vysocanensis* Přibyl and Vaněk; p. 286, pl. 3, figs 1-3.

1994 *Onnia seunesi* (Kerforne); Lebrun, text-fig. 3.

1994 *Onnia seunesi* (Kerforne); Lebrun, pp. 8-11, text-figs 6, 7, 10, 11.

1994 *Onnia grenieri* (Bergeron); Lebrun, pp. 11, 12, 15-17, text-figs 8, 9, 10, 11.

1995 *Deanaspis vysocanensis* (Přibyl and Vaněk); Shaw, pp. 17-19, fig. 14-6, 9-11, 13, 14.

1997 *Deanaspis* aff. *vysocanensis* (Přibyl and Vaněk); Hammann and Leone, pp.65-67, pl. 26, figs 1-8, text-fig. 15.

2001 *Deanaspis vysocanensis* (Barrande); Vanek, p. 42.

Distribution. Sangsurière Formation, Andouille Formation, mid Caradoc, Armorica. Upper "Bancs mixtes", possibly upper Caradoc-Ashgill, Sierra Morena, Spain.

Diagnosis. The Spanish material shows recorded pit counts: E_1, 22-27 (mean, 24), number, 8; I_1, 18.5-22.5 (21), n, 8; I_2, 17-22.5 (20), starting at row 0-3 (2) n, 8; I_3, 10-18, (19), satring at row 5-9 (7), n, 7; I_4, 9-12 (10.5), starting at row 13, n, 3; I_n, 11-15 (14), cut off by arc I_3-I_4 ($I_{3.5}$), n, 7.

Remarks. This substanial synonymy has clarified the distribution of a number of Caradoc species. Most understandably, have been previously wrongly diagnosed on the basis of the strong first internal pseudogirder. All, however, show a strong girder, often broad. The upper lamella is similar to that in *Onnia* and possibly reflects parallel evolution. All the species herein synonymised with *D. pongerardi* are poorly constrained stratigraphically but the literature suggests that they are from the middle Caradoc, with the exception of the Spanish material which is stated to be from the upper Caradoc–Ashgill. There are no morphological differences between the Spanish and Armorican specimens. Cooper and Young in their unpublished theses (1980 and 1985, respectively) described material from the Rosan and Louredo formations of middle to upper Caradoc Series, assigned specimens to *Onnia grenieri*, *O.* cf. *grenieri* and *Deanaspis seunesi*. They all show similar pit count ranges and other features, including the distinct girder and importantly distinct first internal pseudogirder and are here included within *D. pongerardi*. Numerous specimens from Armorica and Spain do not have occipital spines and none are reported for the Bohmenian specimens . Indeed, *D. pongerardi* was originally diagnosed by its lack of this structure. Other marrolithine genera; *Protolloydolithus* and *Hammannaspis* contain species that lack occipital spines.

Deanaspis linol Šnajdr, 1981

Plate 10, Fig. 13.

1981 *Deanaspis linol* Šnajdr, p. 284, Pl. 2, fig. 6, p. 3, fig. 6 [*non* pl. 2, fig 8 = *D. g. goldfussii*]

1995 *Deanaspis linol* Šnajdr; Shaw, p. 15, fig.13-14.

2001 *Deanaspis linol* Šnajdr; Vaněk, p. 46.

Holotype. Partial internal mould of cranidium showing external mould of ventral surface of lower lamella. By original designation; MŠ 11156, from the Libeň Formation, Řevnice Quartzite, Rumpál Mountain near Rokycany, Bohemia.

Other material. Thirty-eight partial cephala and pygidia, some of which are identicle to *Deanaspis goldfussii* (see below).

Distribution. Only found in the Libeň Formation, Řevnice Quartzite, Rumpál Mountain near Rokycany, Bohemia.

Diagnosis. I_2 arc not complete; I_3 short; I_n cut off by I_3; All pits about same width; slightly more E_1 arc pits than I_1 arc. E_1, 28-31; I_1, 21-24; I_2, 19-22, I_2 starting at row 2-3; I_3 starting at row 5-6 (numbers based on two specimens).

Remarks. Šnajdr (1981) misidentified a *Deanaspis goldfussii* specimen as an individual of the new species, *linol*. This confusion along with the premise that *Onnia* was restricted to the upper Caradoc/Ashgill probably led to *linol* being synonymised with *Deanaspis goldfussii* by Shaw (1995). *Onnia linol* differs from *Deanaspis goldfussii* by lacking a complete I_2 arc; I_3 arc beginning more rearwards; I_n is cut off by I_3 and not by I_4 or I_5; increased number of E_1 arc pits compared to I_1 arc. The poorly preserved holotype shows all the characteristics of *Onnia pongerardi*. However, the external cast of the lower lamella is poorly preserved so precise assignment is difficult. It may prove to be synonymous with *Onnia pongerardi* but it is retained as a separate species until better material becomes available.

Genus **ONNIA** Bancroft, 1933

Type species. *Cryptolithus superbus* Bancroft, 1929*b*. Original designation by Bancroft (1933) from the Onny Formation, Onnian, upper Caradoc, from the cliff section, Onny River, south Shropshire, England.

Generic diagnosis. Fringe subsemicircular to subquadrate. E_1 complete and outermost arc. Girder list present; first and second internal pseudogirder lists also present. Girder only weakly developed near genal angles; first internal pseudogirder very prominent, particularly frontally.

Remarks. Hitherto, *Onnia* had only been reported from much younger horizons (upper Caradoc) than those containing *Deanaspis* (lower to middle Caradoc). The present study has demonstrated the occurrence of *Onnia* in the lower Caradoc of Morocco. It had been assumed (Hughes *et al*. 1975, Owen and Ingham 1988, Shaw 1995) that an evolutionary line was reflected in the morpho-series from dominant girder (such as in *Marrolithus*) through equally developed girder and first internal pseudogirder of *Deanaspis* to the condition in *Onnia* with only the first internal pseudogirder dominant. The new discoveries show *Deanaspis* and *Onnia* became established around the Iapetan margin at the same time and therefore, *Onnia* was not derived directly from *Deanaspis*; an interpretation supported by the cladistic analysis (see Section 3.3).

The present study has also shown that the Anglo-Welsh *Onnia superba* (Bancroft, 1929) cannot be separated at species level from the Bohemian *O. ultima* (Barrande, 1852), and a species also recognised herein from Morocco. Shaw (1995) synonymised *Onnia abducta* (Přibyl and Vaňk, 1969) with *O. superba*. It is here regarded as a subspecies of *O. ultima*. *O. ultima* is here interpreted to contain seven geographical and stratigraphical subspecies, including the nominate subspecies and *O. u. abducta* from Bohemia. *O. ultima superba* (Bancroft, 1929) and the other Avalonian subspecies previously included in *O. superba* by Owen and Ingham, 1988, now termed *O. u. cobboldi* (Bancroft, 1929*b*) and *O. u. creta* Owen and Ingham

(1988), the Bohemian *O. ultima abducta* and a new subspecies from Morocco: *Onnia ultima canthyle*.

There are two distinct groups of *Onnia*: the subspecies of *Onnia ultima* which lack I_2 pits in front of the glabella and I_n is cut off by the I_3 arc and a group comprising *Onnia gracilis* (Bancroft, 1929) (here also decribed from the lower Caradoc of Morocco) and *O. pusgillensis* (Dean, 1961) (from the Ashgill of Avalonia) showing I_2 complete and I_n cut off by I_3 or I_4.

Species and subspecies recognized herein:

Onnia ultima ultima (Barrande,1852)

Onnia ultima superba (Bancroft, 1929)

Onnia ultima cobboldi (Bancroft, 1929)

Onnia ultima creta Owen and Ingham, 1988

Onnia ultima abducta Přibyl and Vaněk (1969)

Onnia ultima canthyle sp.nov.

Onnia gracilis (Bancroft, 1929)

Onnia pusgillensis (Dean, 1961)

Onnia etyma sp.nov.

Distribution. *Onnia* is now recognised from the lower Caradoc (Aurelucian) to Ashgill of Morocco and Bohemia and from a short interval (uppermost Caradoc and lowest Ashgill) in the Anglo-Welsh area.

Onnia ultima (Barrande, 1852)

Diagnosis. Cephalic outline subrounded to subangular. E_1 and I_1 arcs complete; I_2 arc not complete frontally; I_3 lacks about 3-10 pits mesially; I_n cut off by I_3; small number of F pits and small intercalated inner pits (less than 20). Pseudogirder dominant frontally, laterally girder and pseudogirder approximately equal.

Remarks. Shaw (1995) synonymised *O. abducta* Přibyl and Vaněk, 1969 with *O. superba superba* (Bancroft, 1929) on the basis of similar pit counts, number of arcs and the starting positions of those arcs. Owen and Ingham (1988) drew attention to the sigmoidal outline of the *O. abducta* pygidium but Shaw (1995) believed that the shape may be due to post burial distortion. There does appear to be a difference in pygidial outline between *O. abducta* and other *Onnia* and until larger samples of the Bohemian taxon are available it is herein placed seperately as a subspecies of *O. ultima*. Shaw (1995) retained *O. ultima* as a separate species from *O. superba* on the basis of the higher E_1 pit counts in the Bohemian species.

Little can be added here to the detailed review of successive Avalonian population samples carried out by Owen and Ingham (1988) who recognised three subspecies of *O. superba* [herein *O. ultima*]: *O. superba superba, O. superba cobboldi* and *O. superba creta*. Local Range Zones were defined on the basis of these subspecies in Shropshire. An explanation of the position of "*O. s. creta*" [herein *O. ultima creta*] on the cladograms Text-figs 3.24 and 25, must be addressed it branches off at a different node from the other two *Onnia superba* [herein *O. ultima*] subspecies. This is due in part to the low pit counts, increased pit width and elevated I1 arc on the upper lamella, of the type specimen of *O. s. creta* [herein *O. ultima creta*] compared to the types of the other subspecies. But there are sufficient specific level characters to warrant it remaining within *O. superba* [herein *O. ultima*], such as; I_n cut off by I_3 arc, I_2 arc is not complete frontally, I_1 pits are large over all fringe and the range of pit numbers in all arcs show overlap with that of the other subspecies.

Owen and Ingham (1988) showed that there are two morphotypes of *O. ultima superba* in Avalonia. These can be distinguished by their E_1 pit counts. Higher pit counts were observed in younger samples than was the case in older ones. A similar trend is seen within the Bohemian material between *Onnia ultima abducta* and the later *O. u. ultima.* A possible case was discounted within the Moroccan samples after scatter graph represntation of the data showed a continuous range of pit counts, see later.

Onnia ultima ultima (Barrande, 1852)

Plate 11, Fig. 2.

1852 *Trimucleus ultimus* Barrande, p. 631, pl. 29, figs 18-20.

1969 *Onnia ultima* (Barrande); Přibyl and Vaněk, p. 111, pl. 10, figs, 1 -10, pl. 15, figs 7,8.

1995 *Onnia ultima* (Barrande); Shaw, p. 20, figs 15.10, 15.11, 15.14-15.17.

Holotype. Partial dorsal surface of a juvenile cephalon. Designated by Přibyl and Vaněk (1969); ČD 1672, from, Králův Dvůr Formation, Ashgill Series, Králův Dvůr near Beroun, Bohemia. Figured by Barrande (1852) on pl. 29, figs 18, 19.

Distribution. Králův Dvůr Formation, Ashgill Series, Prague Basin. Czech Republic.

Diagnosis. E_1, I_1, and I_n complete frontally, I_2 starts at row 2-3, I_3 starts around row 8, I_n cut off by I_3. I_1 pits large over fringe I_2 and occasionally I_3 pits increase in size to equal I_1 posteriorly. Low inflation posteriorly on upper lamella of I_1 and I_2 arcs. Lower lamella shows first internal pseudogirder prominent over fringe; no girder or second internal pseudogirder. Recorded data: E_1, range 20-31.5 (mean = 25); I_1, 16-24 (19.5); I_2, 13-21 (17) start at I_n row, 1-5 (3); I_3, 6-18 (12), start at I_n row, 3-14 (8.7); I_n, 10-17 (14).

Remarks. O. u. ultima and *O. u. superba* show similar features such as: lack of I_2 mesially, I_n cut off by I_3 arc and I_1 pits wider than other arcs. Never the less *O. u.*

ultima does show a number of differences; on the lower lamella the first internal pseudogirder is prominent around the whole fringe with only slight development of the second internal pseudogirder and girder. On the upper lamella there is a low inflation posteriorly which is centred on the I_1 and I_2 arc. These consistent differences warrant subspecific separation of the Anglo-Welsh material.

Onnia ultima superba (Bancroft, 1929*b*)

Plate 11, Fig. 1.

1929*b* *Cryptolithus superbus* Bancroft, p. 95, pl. 2, fig.10.

1933 *Onnia superba* Bancroft, table 1 (*non* Dufton Shale specimens = *O. pusgillensis* Dean, 1961b)

1960 *Onnia? cobboldi* (Bancroft); Dean, pl. 19, fig. 1.

1960 *Onnia superba* (Bancroft); Dean, pp. 133-136, pl. 19, figs 4-6, 8, 9, 11, 13, 14.

1960 *Onnia* aff. *superba* (Bancroft); Dean, pp. 136, 137, pl. 19, fig. 10.

1975 *Onnia superba* (Bancroft); Hughes *et al.*, pl. 9, fig. 107.

1979*b* *Onnia superba* (Bancroft); Hurst, p. 210, fig. 36.

1988 *Onnia superba* (Bancroft); Morris, p. 155.

1988 *Onnia superba superba* (Bancroft); Owen and Ingham, p. 844, pl. 74, figs 1-13, text-figs, 1, 3-6, table 1.

non 1995 *Onnia superba* (Bancroft); Shaw, pp. 19, 20, figs 15. 1-15.9.

1996 *Onnia superba superba* (Bancroft); Owen and Ingham, pp. 148, 149, pl. 26, figs 14-16.

Holotype. Internal mould of a cephalon; NHM In42070, from the upper part of the Onny Formation, upper Onnian, cliff section, Onny River, south Shropshire, England.

Distribution. Within the river section of the upper 24 m of the type Onnian Stage, lowest *linearis* Biozone, extending across the boundary of the Acton Scott and Onny formations constituting the *Onnia superba superba* Local Range Zone; see Owen and Ingham 1988).

Diagnosis. Fringe moderately declined from laterally area to posterior. I_2 arc not complete, up to 3 pits missing mesially; I_3 lacks 3-9 pits mesially; I_n cut off by I_3 arc. I_1 and I_2 arcs increase in width to posterior margin. E_1, about 20-29.5; I_1, about 15.5-22.5 pits. Pseudogirder dominant frontally becoming poorly developed posteriorly; girder present posteriorly leading to genal spine ridge.

Remarks. The girder is present only near the genal angle and has led in the past to misinterpretation of the pseudogirder and girder. The range in pit counts for E_1 show variation between early and late samples of the subspecies, although these ranges do overlap. The Bohemian samples previously ascribed to *O. superba* (Shaw 1995) are reidentified as belonging in *O. u. ultima*.

Onnia ultima cobboldi (Bancroft, 1929*b*)

Plate 11, Figs 8, 10-12.

1929*b* *Cryptolithus cobboldi* Bancroft, p. 92, pl. 2, figs 6, 7.

1960 *Onnia? cobboldi* (Bancroft); Dean, pp. 128-132, pl. 19, figs 3, 12.

1975 *Onnia cobboldi* (Bancroft); Hughes *et al.*, pl. 9, figs 104-106.

1979*a* *Onnia cobboldi* (Bancroft); Hurst, pp. 204, 227 only samples 97, 98, fig. 16.11.

1979*b* *Onnia cobboldi* (Bancroft); Hurst, p. 210, fig 37.

1983 *Onnia cobboldi* (Bancroft); Owen, pl. 34, figs 1, 5.

1988 *Onnia cobboldi* (Bancroft); Morris, p. 155.

1988 *Onnia superba cobboldi* (Bancroft); Owen and Ingham, pp. 844, 845, pl. 75, figs 1-11, text-figs 1, 3-6, table, 1.

2000 *Onnia superba cobboldi* (Bancroft); Owen *in* Rushton *et al*, p. 278.

Lectotype. Incomplete cephalon; BNHM In42074, from the upper part of the Wistanstow Member of the Acton Scott Formation, lower Onnian, Onny River section, south Shropshire.

Material. Numerous testiferous specimens from the Onny Valley, single testiferous cranidium from Northern England and around 30 cephala, cranidia and lower lamellae from Morocco.

Distribution. Short stratigraphical range in the upper part of the *clingani* Biozone of the Onny Valley; however, the range of the subspecies has now been extended from Shropshire with the identification of a single specimen from Dufton Shale Formation, upper Caradoc Series, Onnian Stage, Pus Gill, Cross Fell Inlier, Northern England (see Pl. 11, Fig. 8). Sandstones of the Upper Ktaoua Formation, Ktaoua Clay and Sandstone Group, the lowest Ashgill Series, Jbel bou Debgane, Bou Haiara, Zegdou, Anti Atlas Mountains, Morocco.

Diagnosis. I_2 arc absent mesially, up to 3 pits missing mesially; I_3 lacks about 3-10 pits mesially; I_n cut off by I_3 arc. I_1 and I_2 arc pits increase in width to the posterior margin. E_1, about 18-26.5; I_1, about 14-22.5 pits. Pseudogirder dominant over all fringe; girder apparent as narrow ridge over fringe.

Remarks. E_1 pits are not as crowded as in *O. u. superba.* In well-preserved specimens distinct curvature of posterior area of fringe seen. The distinct girder list and first and second internal lists allow for the subspecific separation from *O. u. superba.* The Moroccan specimens show an increase in pit diameter of I_1 arc frontally that is not as distinct in the Anglo-Welsh samples. This feature is here not regarded as sufficient to warrant separation from *O. u. cobboldi.* The identification of a single

specimen from Northern England and samples from Morocco have extended the range of this subspecies.

Onnia ultima creta Owen & Ingham, 1988

Plate 11, Fig. 9.

1979*a* *Onnia cobboldi* (Bancroft); Hurst (*pars*), pp. 204, 227 (samples 35, 99-102).

1979*b* *Onnia cobboldi* (Bancroft); Hurst (*pars*), p. 210 (*pars*).

1988 *Onnia cobboldi creta* Ingham & Owen; Morris, p. 155 [*nomen nudum*, see Owen and Ingham 1988, p. 855]

1988 *Onnia superba creta* Owen and Ingham, pp. 845,848, pl. 76, figs, 1-9, text-figs, 1, 3--7, table 1.

Holotype. A testiferous cephalon; GLA HM A15087, from 14.8 m above the base of the Onnian Stage, upper Acton Scott Formation (*O. s. creta* Local Range Zone), Onny River section, south Shropshire, England.

Distribution. Upper Acton Scott Formation (*O. s. creta* Local Range Zone), Onnian Stage, upper part of the *clingani* Biozone, Onny River section, south Shropshire, England.

Diagnosis. I_2 arc absent mesially by up to 4 pits. I_3 lacks between 3-10 pits frontally; I_n cut off by I_3. Extreme pit width increase of arc I_1 and arc elevation from the lateral region to the posterior margin; fringe markedly convex along strong lists either side of I_1 laterally. E_1, about 14-23 (mean); I_1, about 15-20.5 (mean) pits. Pseudogirder dominant over fringe; girder present as narrow ridge frontally and posteriorly but not laterally.

Remarks. *O. u. creta* is closely related to *O. u. cobboldi* with I_2 arc absent mesially, I_n cut off by I_3, I_1 arc increasing in pit width towards the posterior margin and the lower lamella structures all show close similarities to *O. u. superba.* The separation of *O. u. creta* from the other Avalonian *ultima* subsbpecies on the cladograms (Text-figs 3.24 and 3.27) is due to the raised I_1 arc, not seen in the other two subspecies.

Onnia ultima abducta (Přibyl and Vaněk, 1969)

Plate 11, Fig. 4.

1969 *Cryptolithus abductus* Přibyl and Vaněk, p. 105, pl. 6, figs 5-16.

1975 *Onnia abducta* (Přibyl and Vaněk); Čech, pl. 3, figs 1, 2, 4, pl. 4, figs 1, 2, 4.

1980 *Onnia abducta* (Přibyl and Vaněk); Přibyl and Vaněk, pl. 3, figs 4-6.

1995 *Onnia ultima* (Barrande); Shaw, p. 20, figs 15.10, 15.11, 15.14-15.17.

Holotype. Complete internal mould of cephalon. Original designation; UUG JV 954 (3190) from Bohdalec Formation, Velka Chuchle, Bohemia.

Distribution. Only found within the Bohdalec Formation of the Prague Basin, Czech Republic.

Diagnosis. E_1, I_1, and I_n complete frontally, I_2 starts at row 2-3, I_3 starts around row 8, I_n cut off by I_3. I_1 pits large over fringe I_2 and occasionally I_3 pits increase in size to equal I_1 posteriorly. Low inflation posteriorly on upper lamella of I_1 and I_2 arcs. Lower lamella shows first internal pseudogirder prominent over fringe; no girder or second internal pseudogirder. Pygidium shows distinctive sigmoidal posterior outline. Recorded data: E_1, range 23-28 (mean = 25.5); I1, 16-23 (19).

Description. As for *O. u. ultima* except for lower pit count in E_1 arc and distinctive posterior sigmoidal outline of the pygidium.

Remarks. The lower E_1 pit counts and distinctive sigmoidal pygidial outline differentiate *O. u. abducta* from *O. u. ultima.* This stratigraphical trend to higher E_1 pit counts mirrors that in *O. u. superba.* Shaw (1995) synonymised *O. abducta* with *O. superba superba*, although he did state that subspecific designation was difficult. Shaw also noted that Owen and Ingham (1988) regarded the pygidia of the English and Bohemian material to be different. Shaw went on to state that the majority of material shows some distortion and the importance of the pygidial shape is unclear. The sigmoidal posterior pygidial outline is seen particularly well in specimens of dorsal surface internal moulds (Pl. 11, fig. 4). The range of pit counts for *O. u. abducta* and *O. u. ultima* show a continuous range, the former at the lower range and the latter at the higher end. The lower pit counts seen in *O. u. abducta* and the pygidium outline are sufficient to retain this species as separate from *O. u. ultima.* The Moroccan material is synonymised herein with *O. u. abducta* on the basis of the following features: I_2 arc not complete, up to 3 pits missing mesially; I_3 lacks 3-9 pits mesially; I_n cut off by I_3 arc. I_1 and I_2 arcs increase in width to posterior margin. E_1, 20-29.5; I_1, 15.5-22.5 pits. Girder and first and second internal lists become broad posteriorly; fringe becomes convex posteriorly producing a low inflation centred on the I_2 arc. Pseudogirder dominant frontally becoming poorly developed posteriorly; girder present posteriorly leading to genal spine ridge. There are no unique features of the Moroccan specimens.

Onnia ultima canthyle sp nov.

Plate 11, Figs 3, 5-7.

Derivation of name. swelling

Holotype. Nearly complete testiferous cranidium, MNM 11/1, from the upper-middle siltstones of the Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, upper Caradoc Series of Bou R'bia – Sidi Touhama, Coude Du Dra, Anti Atlas Mountains, Morocco.

Other material. Abundant cephala, cranidia, thoracic segments and pygidia together with rare more complete individuals.

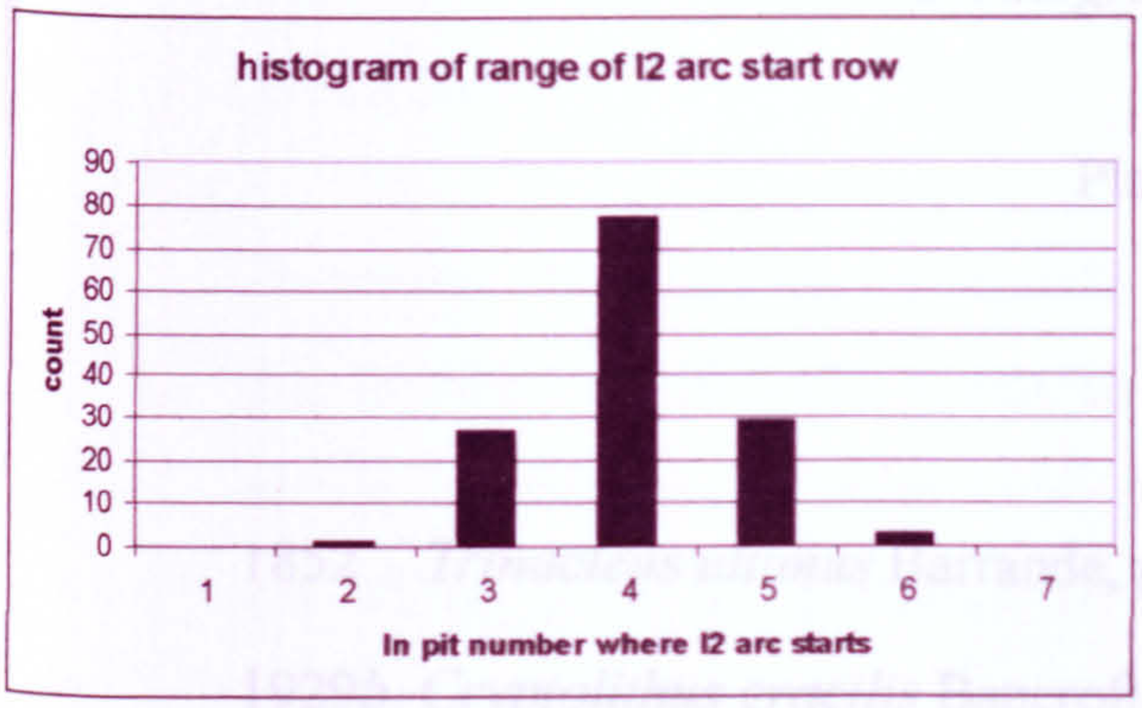
Distribution. From the upper-middle siltstones of the Lower Ktaoua Formation to uppermost Rouid Aissa and Upper Tiouririne sandstone members, Ktaoua Clay and Sandstone Group, upper Caradoc and lower Ashgill series of Bou R'bia – Sidi Touhama, Coude Du Dra; north of Rabt el Hajar-Tafilalt and Taguerroumt, W of Tafilalt, Erfoud district; anticline of Jbel Mimount, Tarhbalt district, Anti Atlas Mountains Morocco.

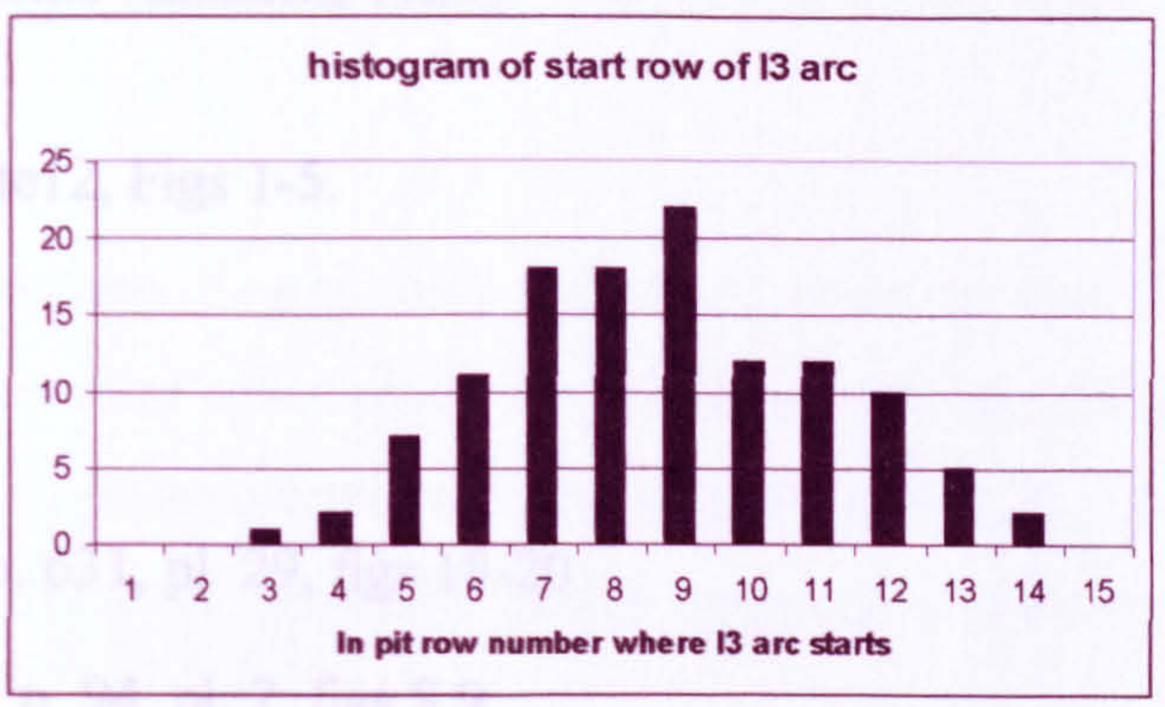
Diagnosis. I_2 arc not complete, up to 3 pits missing mesially; I_3 lacks 3-9 pits mesially; I_n cut off by I_3 arc. I_1 and I_2 arcs increase in width to posterior margin. E_1, 20-29.5; I_1, 15.5-22.5 pits. Girder and first and second internal lists become broad posteriorly; fringe becomes convex posteriorly producing a low inflation centred on the I_2 arc. Pseudogirder dominant frontally becoming poorly developed posteriorly; girder present posteriorly leading to genal spine ridge.

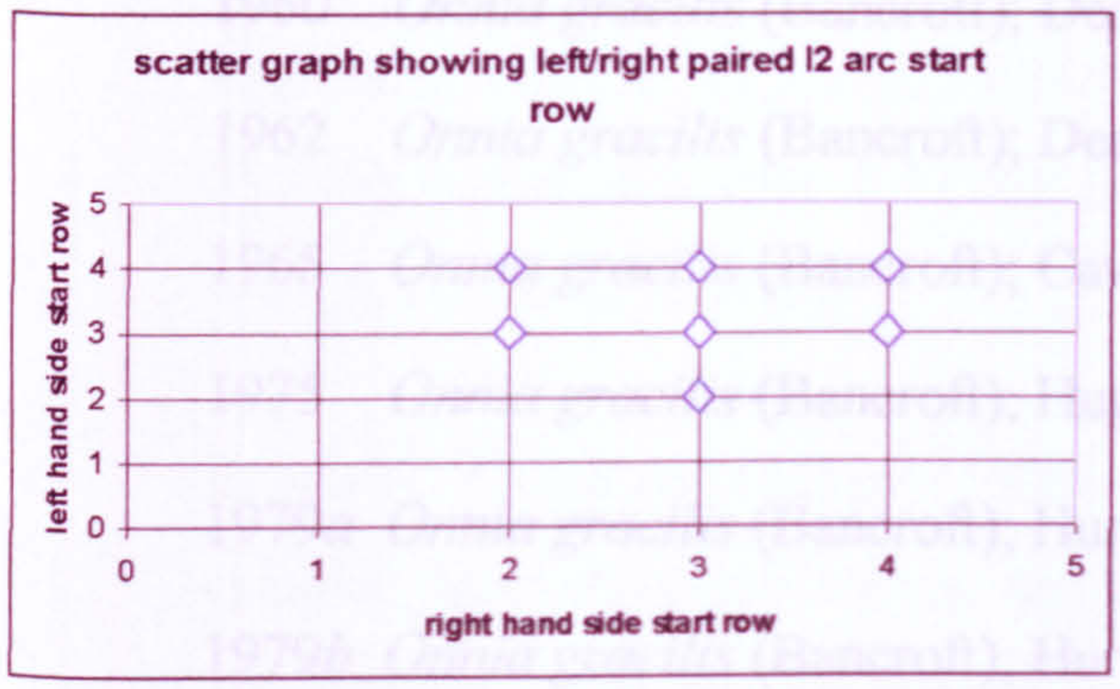
Description. Subrounded cephalon. Moderate anterior arch. Glabella swollen, clavate median tubercle present, one pair of faint lateral furrows P1, apodemal pits shallow. Occipital furrow shallow and narrow (sag.) with short, sharply tapering

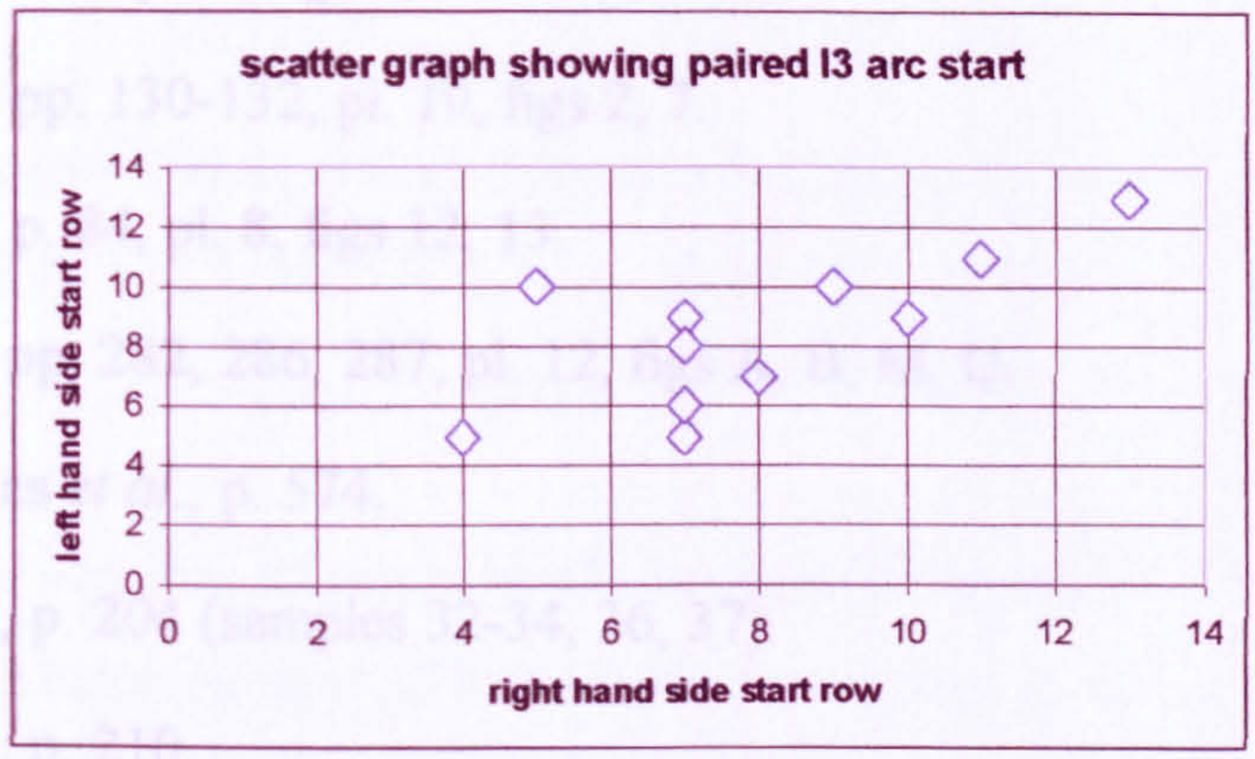
occipital spine. Axial furrows broad and moderately deep, hypostomal pit small and shallow. Rounded genal lobes, declining steeply to fringe. Fringe broad and gently convex from lateral position to posterior, slight inflation of posterior region centred on arcs I_1 and I_2, the last few pits (2-3) of each arc not being involved in the inflation. E_1 pits smaller and closer together than I_1 pits. I_1 pits are large and only marginally increase in size towards the posterior margin, I_2 pits increase in size to match I_1 pit size near posterior margin. Girder and first internal lists prominent over fringe, second internal list clear posteriorly. E_1, I_1 and I_n arcs complete frontally, I_2 arc starts around row 2-4, I_3 starts around row 6-11, I_n is cut off by I_3 arc. Often the exact cut off point in difficult to distinguish on the upper lamella as I_n, I_3 and F pits are close and often sulcate, seen more clearly on the lower lamella. Low number of F pits and small intercalated inner pits (less than 15). Lower lamella shows distinct first internal pseudogirder frontally but which is weakly developed laterally and posteriorly. Girder only weakly developed over fringe. Second internal pseudogirder dominant posteriorly. Strong channel from first internal pseudogirder and girder leads to genal spine. Genal spines gently curve inwards.

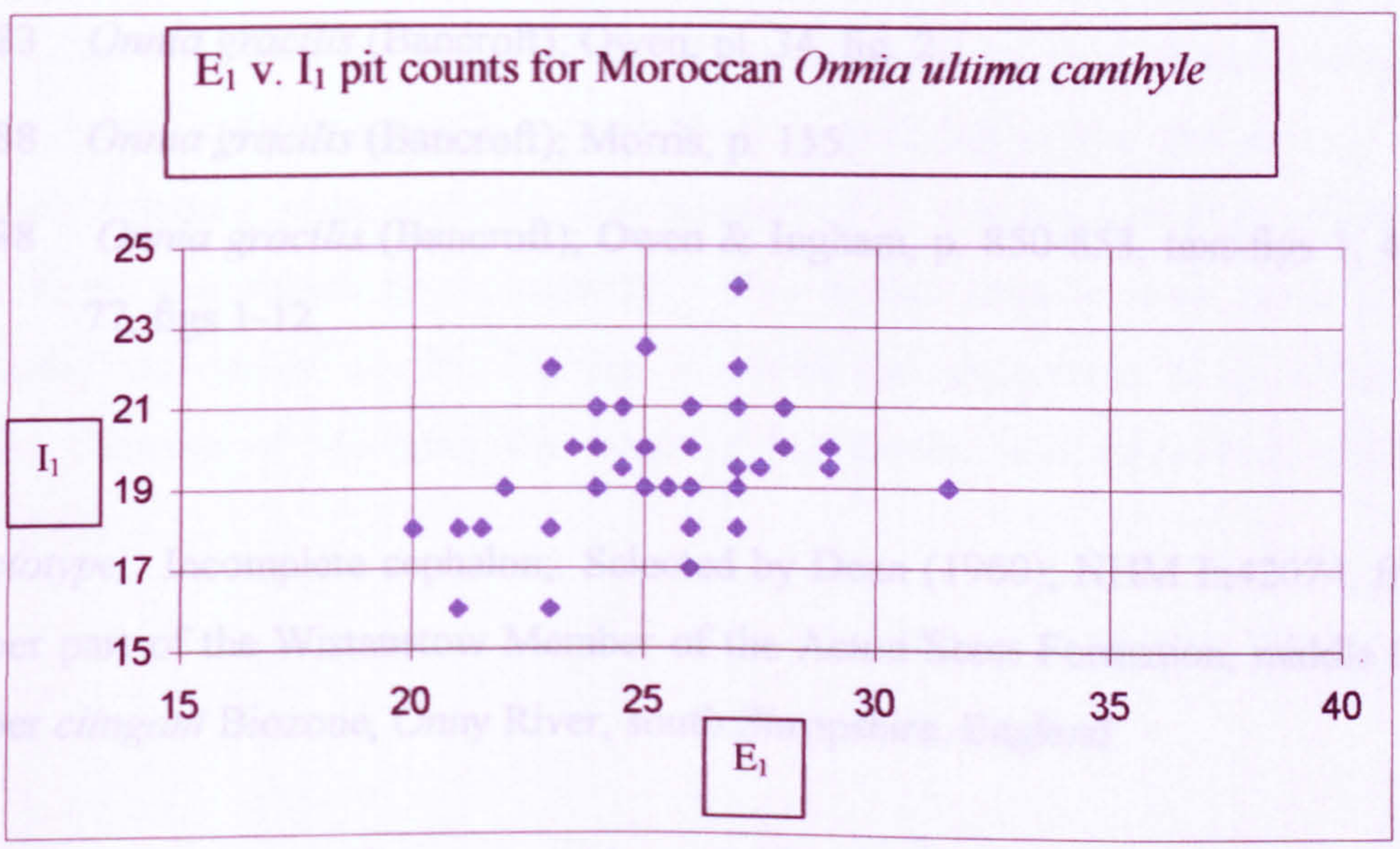
Remarks. It has long been recognised that cryptolithine trinucleid trilobites show asymmetry about the left and right halves of the fringe for all arcs. This is also the case in the marrolithines. Analysis of the abundant testiferous material has enabled comparison of the starting postion of the internal arcs I_2 and I_3 on either side of the fringe, the results show the majority of specimens show asymmetry on the starting points of these arcs (see Text-Fig. 4.18). Scatter graph of the E_1 pit count against the I_1 pit count shows a range of variation (see Text-Fig. 4.18). During data collection an apparent trend to higher E1 pit counts compared to the I1 arc of the same individual was perceived, this, however, proved false when a scatter graph was produced, Text-Fig. 4.18.











Text-Fig. 4.18 shows various graphical represntations of pit count data for *O. u. canthyle* sp. nov.

Onnia gracilis (Bancroft 1929)

Plate12, Figs 1-5.

1852 *Trimucleus ultimus* Barrande, p. 631, pl. 29, figs 18-20.

1929*b* *Cryptolithus gracilis* Bancroft, p. 94, pl. 2, figs 8,9.

1960 *Onnia gracilis* (Bancroft); Dean pp. 130-132, pl. 19, figs 2, 7.

1962 *Onnia gracilis* (Bancroft); Dean p. 84, pl. 8, figs 12, 13.

1965 *Onnia gracilis* (Bancroft); Cave pp. 282, 286, 287, pl. 12, figs A, B, M, Q.

1975 *Onnia gracilis* (Bancroft); Hughes *et al.*, p. 574.

1979*a* *Onnia gracilis* (Bancroft); Hurst, p. 204 (samples 32-34, 36, 37).

1979*b* *Onnia gracilis* (Bancroft); Hurst, p. 210.

1983 *Onnia gracilis* (Bancroft); Owen, pl. 34, fig. 2.

1988 *Onnia gracilis* (Bancroft); Morris, p. 155.

1988 *Onnia gracilis* (Bancroft); Owen & Ingham, p. 850-853, text-figs 1, 4, 8, pl. 77, figs 1-12.

Lectotype. Incomplete cephalon;. Selected by Dean (1960); NHM In42074, from the upper part of the Wistanstow Member of the Acton Scott Formation, middle Onnian, upper *clingani* Biozone, Onny River, south Shropshire, England.

Distribution. *O. gracilis* occurs with graptolites indicative of the *clingani* Biozone at Welshpool and was interpreted as being Onnian in age by (e.g. Rushton *et al.*, 2000, p.215) *Onnia gracilis* is a stratigraphically long ranging species from the Ouaouglout Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lowest Caradoc Series, (= Aurelucian Stage), Alkhikh-Tazzarine, Tarbolt distrct, Anti Atlas Mountains, Morocco to the topmost Upper Ktaoua Formation, upper Ktaoua Clay and Sandstone Group, (= Rawtheyan Stage), Jbel bou Dedgane, Bou Haiara, Zegdou

district, Anti Atlas Mountains, Morocco. Middle to upper Streffordian of the Anglo-Welsh area.

Diagnosis. Subsemicircular cephalic outline. E_1 pits small and more numerous than I_1 pits (30-41.5 cf. 19.5-27); I_1 pits larger than other pits and vary little in width along arc; I_2 pits become the same width as I_1 posterolaterally. I_2 arc complete frontally. I_n cut off by I_3 or I_4. Pseudogirder prominent frontally, girder apparent posteriorly leading to genal spine.

Moroccan material: E_1, range 25-36 (mean = 29); I_1, 18-24 (21), I_2, 18-25 (21); I_3, 10-19 (16), I_3 start at I_n row, 4-11 (6); I_4, 3-12 (7), I_4 start at I_n row, 12-14 (13); I_n 13-19 (15), I_n cut off by I_4, rarely I_5

Remarks. Owen and Ingham (1988) showed that stratigraphically younger *O. gracilis* samples, from the Onny Valley, had a greater number of individuals possessing an I_4 arc than did older samples whose specimens showed the majority only had I_3. The early Caradoc samples from Morocco show I_n cut off by I_4 in all specimens and the later Ashgill samples show I_n cut off by I_4 in over half of the specimens. I_2 arc is present frontally in the majority of specimens of *O. gracilis*, however, juveniles may not show a complete I_2 arc mesially. This is also seen in some early Moroccan holaspid individuals, see Pl. 12, Fig. 5. With the recognition of *O. gracilis* from lower Caradoc of Morocco, the range of the species now extends throughout the Caradoc.

Onnia pusgillensis Dean, 1961

1933 *Onnia superba* Bancroft, table 1

1948 *Onnia superba* (Bancroft); Lamont, p. 416.

1959 *Onnia* cf. *superba* (Bancroft); Dean, pp. 200, 207.

1961b *Onnia superba pusgillensis* Dean, p. 120, pl. 7, figs 1-5 (*non* fig. 6, ? = *Tretaspis ceriodes alyta* Ingham, 1970)

1962 *Onnia superba pusgillensis* Dean, p. 84, pl. 8, figs 5, 7, 9, 10.

1966 *Onnia superba pusgillensis* Dean; Ingham pp. 464, 486, 497.

1974 *Onnia superba pusgillensis* Dean; Ingham pp. 60-63, pl. 10, figs 1-18, text-figs 20, 21.

1975 *Onnia superba pusgillensis* Dean; Hughes *et al.*, p. 574, pl. 9, fig. 108.

1988 *Onnia superba pusgillensis* Dean; Morris, p. 155.

1988 *Onnia superba pusgillensis* Dean; Owen and Ingham, pp. 852, 853, text-fig. 2.

Holotype. By original designation; NHM In55707, from the Dufton Shales, upper Caradoc Series, Streffordian Stage from the Pus Gill, Cross Fell Inlier, Cumbria, N. England.

Distribution. Restricted to the Dufton Shales, upper Caradoc Series, Streffordian Stage Cross Fell Inlier.

Diagnosis. I_2 arc complete; I_3 lacking 3-5 pits mesially; I_4 present, terminating I_n. Pseudogirder dominant frontally; 2nd pseudogirder most dominant laterally, girder present posteriorly.

Remarks. *O. pusgillensis* specimens are generally poorly preserved and appear to be restricted to northern England. They show characteristics of both the ultima and gracilis stocks, possibly representing a local hybrid.

Onnia etyma sp. nov.

Plate12, Figs 6-8.

Holotype. Internal mould of partial cranidium, MGS 1604/1 from siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series, Bou R'bia –Sidi Touhama, Coude du Dra, Anti Atlas Mountains, Morocco

Other material. Twenty fragments of mainly internal moulds of cranidia, lower lamellae and pygidia.

Distribution. From siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series (Aurelucian Stage), Bou R'bia –Sidi Touhama, Coude du Dra; Mizgarn, Anti Atlas Mountains, Morocco and from Letná Formation, Beroun Series, (equivalent to Caradoc Series, Burrellian Stage) of the Prague Basin, Czech Republic.

Diagnosis. I_2 arc complete; I_3 lacking 3-5 pits mesially; in rare cases I_4 is present and terminates I_n, generally, however, I_n is usually cut off by I_3. All pits in all arcs approximately the same width, no pit inflation. Pseudogirder dominant frontally; 2nd pseudogirder most dominant laterally, girder present posteriorly.

Description. Subrounded cephalic outline with moderate anterior arch. Swollen clavate glabella, shallow occipital furrow and pits, narrow (sag.) occipital ring leading to sharply tapering occipital spine. Axial furrows broad with moderate depth, distinct hypostomal pits. Swollen genal lobes declined steeply towards fringe. Narrow (sag.) posterior border furrow and border, moderate posterior border extension. Fringe narrowest mesially with no localised inflations or raised arcs. Narrow girder list. Three arcs present mesially (I_n, I_1 and E_1), I_2 starts in front of the glabella (about R 4). I_3 starts at about R 9 and I_4 about R11. I_n generally cut off by I_4, rarely by I_3. E_1 pits closely packed and smaller than I_1 pits. I_1 arc pits are approximately the same size

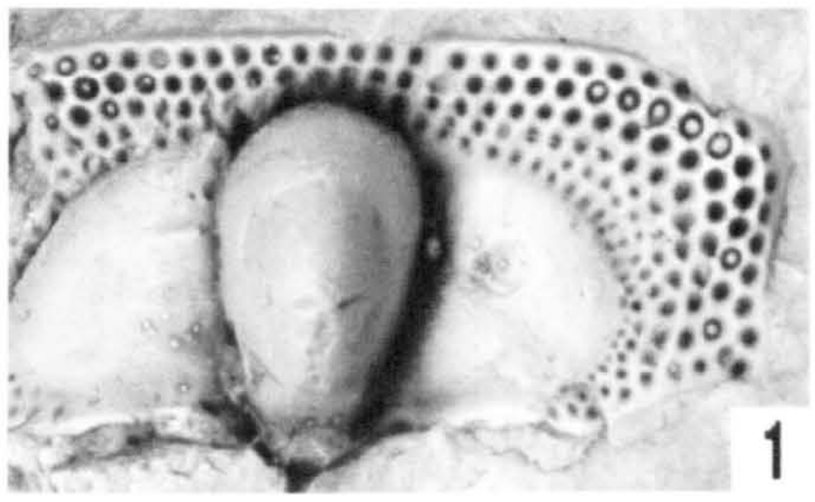
along entire arc. I_2 increases in pit size towards the posterior margin to match I_1 pit sizes. Radial alignment of pits in I arcs until close to posterior margin. Girder weakly developed, first internal pseudogirder prominent frontally. No development of girder or pseudogirder posteriorly. Ventral surface of lower lamella inwardly steeply concave posterolaterally and internal to I_2 arc. Prominent ridge from first internal pseudogirder and girder to genal spine. Fine reticulation over entire glabella and genal lobes in small cephala.

Remarks. This is the earliest *Onnia*, extending the range of the genus down to the lower Caradoc Series. *O. etyma* shows the characteristic strong first internal pseudogirder but lacks enlargment of any pits that is seen in other *Onnia* species.

Plate Descriptions

Explanation of Plate. 1

Figs 1-8. *Marrolithus favus favus* (Salter, 1847). 1. BNHM It 126, latex cast of external mould of cranidium, figured by Oehlert (1895, pl. 1. fig. 1 [= syntype *M. bureaui* (Oehlert, 1985) original housed at Rennes University , France), X3. 2., BNHM It 9622, latex cast of partial external mould of tectonised cranidium showing variation in its fringe inflations. From Lower Llandeilo Flags Formation, Upper Llanvirn Series, Llandeilian Stage, upper *teretiusculus* Biozone from quarry 91m north Ty-gwyn Farm, 805m east of Llandeilo, Carmarthenshire, Wales, X 5. 3-4., From the Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from 73m north Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys. 3., SM A 46910/2, latex cast of tectonised cephalon, X5. 4., SM 46910/1, latex cast of tectonised cephalon on same slab as 3 but in different orientation; note variation in fringe inflations, figured by MacGregor (1963, pl. 116, fig. 21 [= *Marrolithoides* cf. *arcuatus*]), X5. 5., BNHM It 9619, latex cast of tectonised external mould of cephalon. From the Lower Llandeilo Flags Formation, Upper Llanvirn Series, Llandeilian Stage, upper *teretiusculus* Biozone from 18m southeast of Careg-y-foel-gam Farm, 3.22km SSE of Llangadog, Carmarthenshire, X5. 6., SM A46901a, latex cast of external mould of tectonised cephala, figured by MacGregor (1963, pl. 117, figs 5, 6 [= *Marrolithus favus*]). From Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from 183m northwest of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys, X5. 7., BGS 93010a, latex cast of external mould of tectonised cephalon, figured by Whittard (1956, pl. 8, fig. 3 [= paratype of *Marrolithus inornatus* Whittard, 1956]). From Upper Rorrington Shale Formation, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, lower *gracilis* Biozone from Meadowtown; Holywell Brook, 64m southeast of bridge, 229m W7°S Rorrington Green, Shropshire, England, X5. 8., BNHM It 9647, partial silicified cephalon showing lateral margin extension, tubercles on inflated area and invagination of lateral margins as seen in *Marrolithoides* and *Hammannaspis* gen. nov. species. From middle Hendre Shale Formation, Lower Caradoc Series, Aurelucian Stage, Velfreyan Substage, lower *gracilis* Biozone from middle road section, south of Meidrim, St. Clears, Carmarthenshire, Wales, X6.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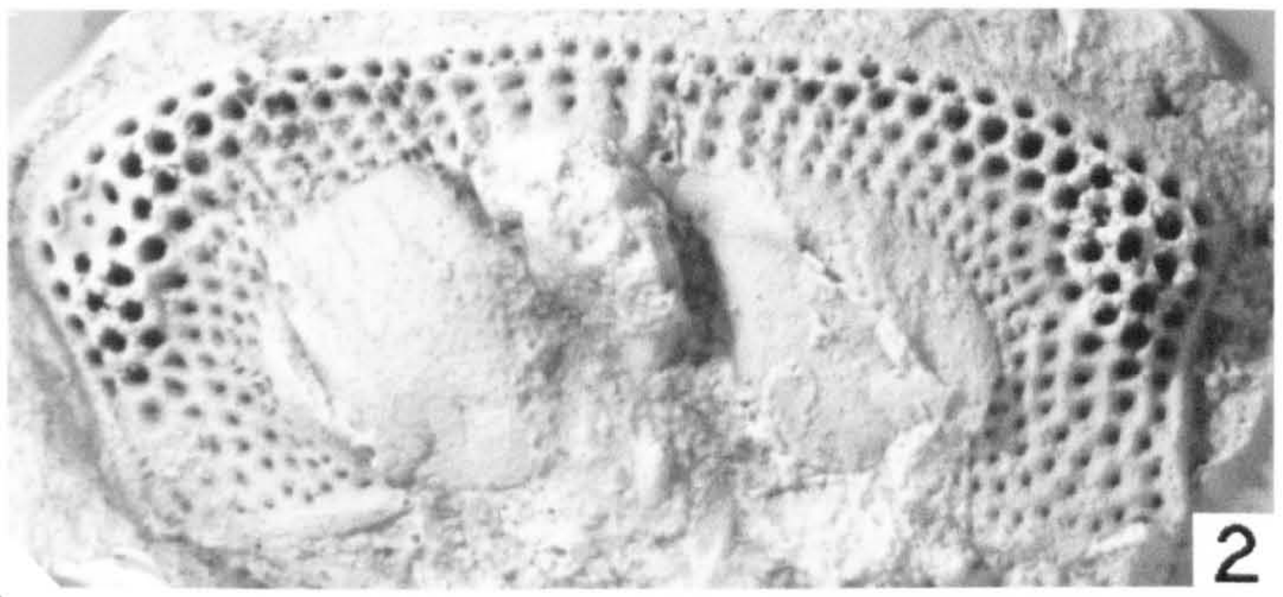
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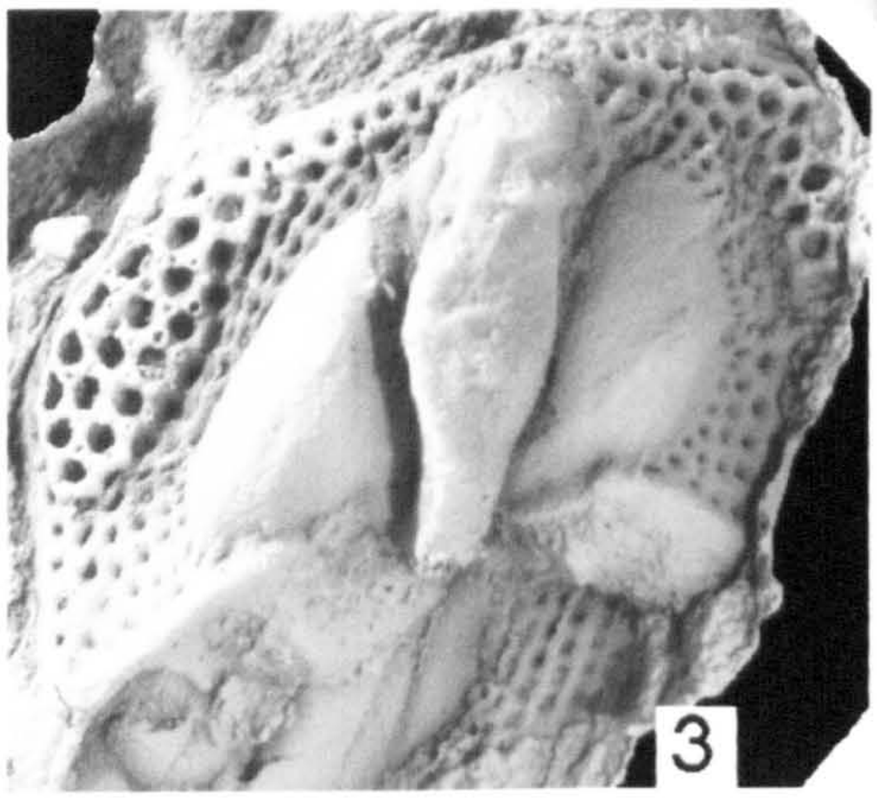
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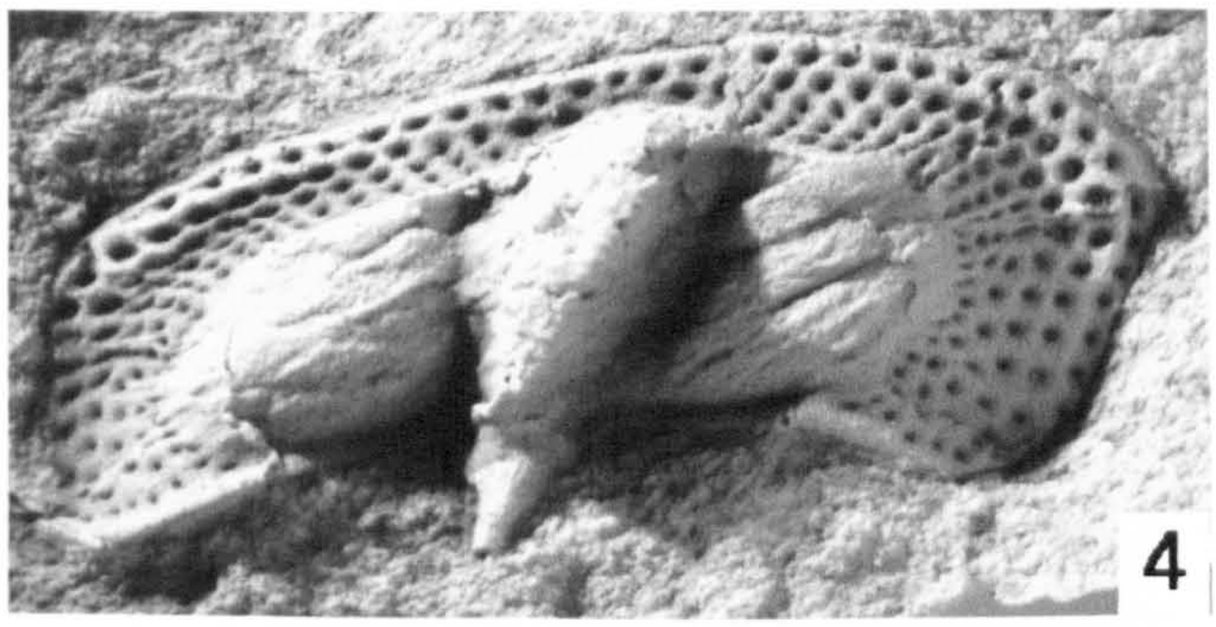
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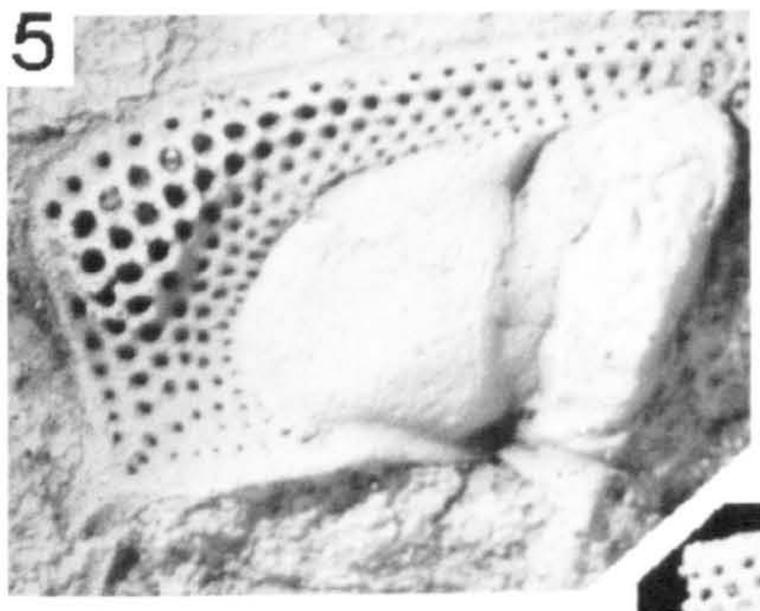
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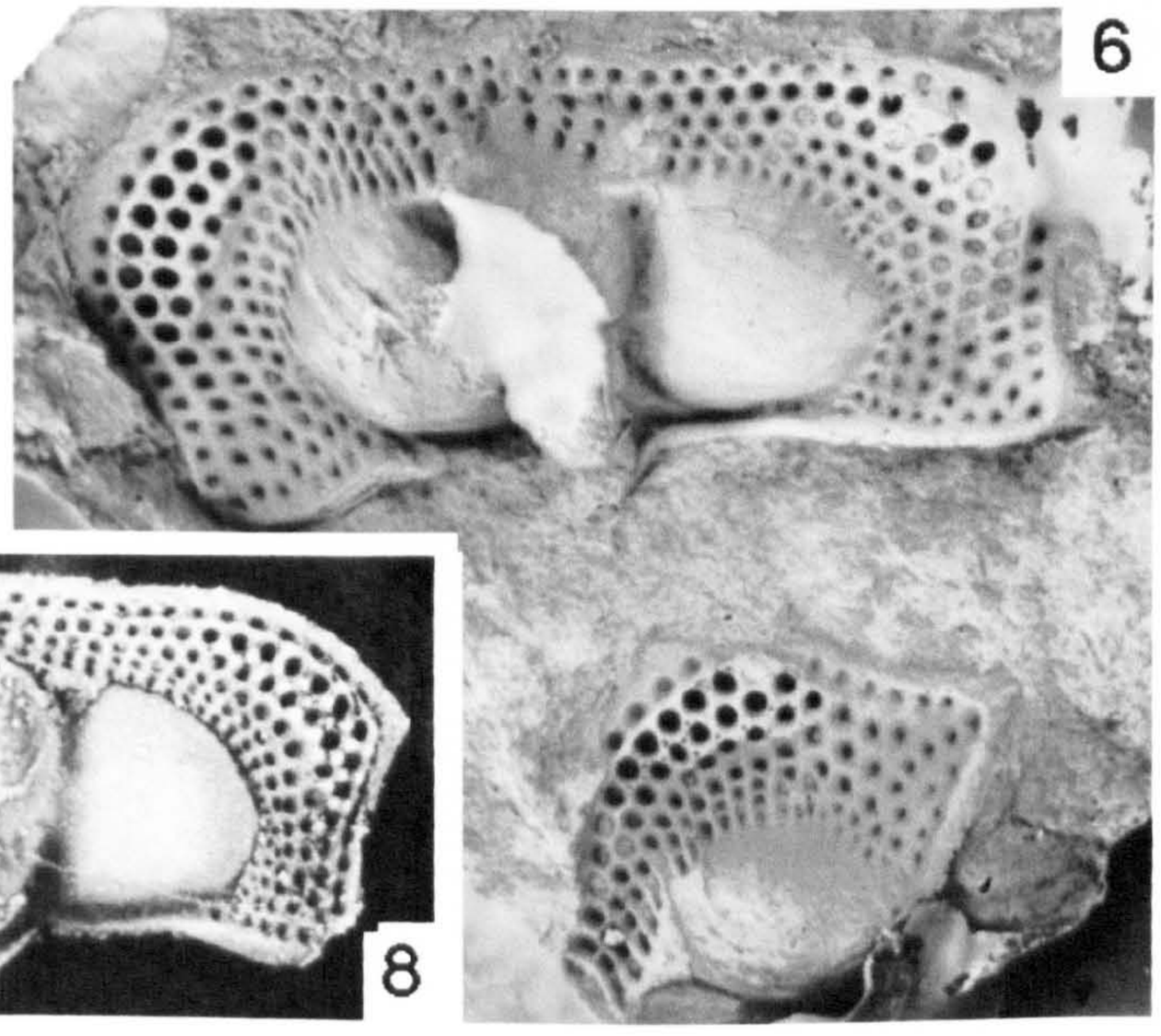
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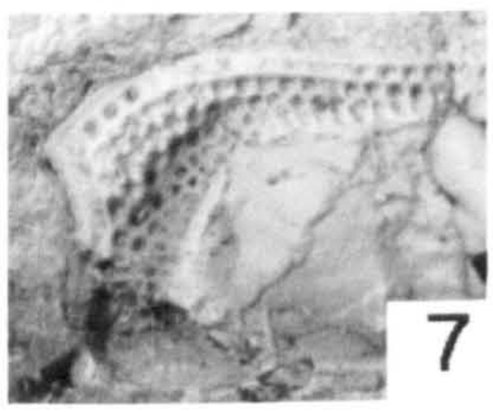
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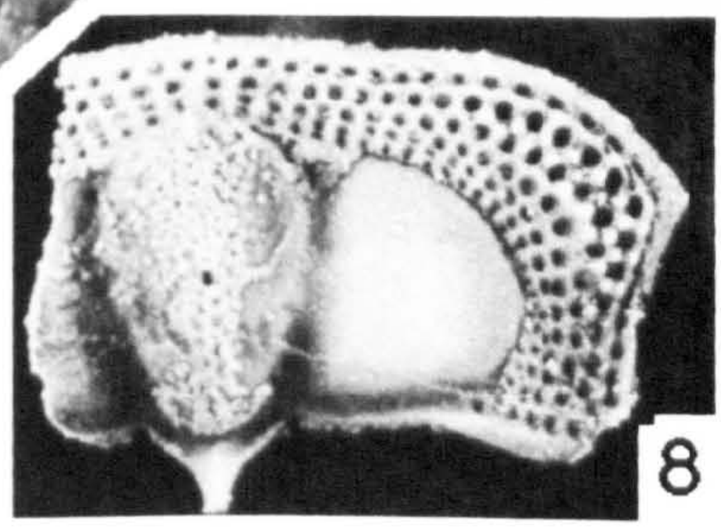
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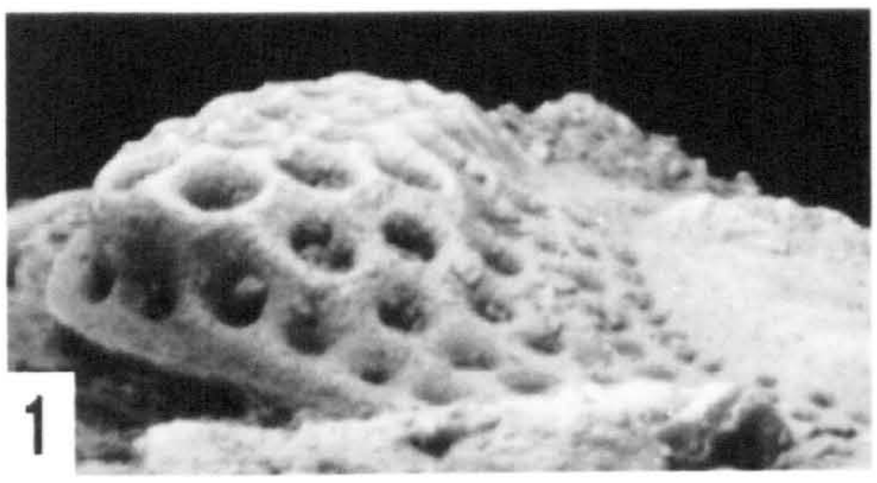
Explanation of Plate. 2

Figs 1-2., *Marrolithus favus magnificus* MacGregor, 1963, Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from Plas-yn-glyn, Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys, Wales. 1., SM A46902/2b, latex cast of partial cranidium showing extreme elevation of internal arc pits. 2. SM A46902b holotype, SM A53014b paratype, SM A53013b paratype (respectively from top), latex cast of external mould of partial cranidia, figured by MacGregor (1963, pl. 117, figs 1-3 [= *M. magnificus*]). 3-5., from Craig-y-glyn Group, Lower Caradoc Series, Lower Aurelucian Stage, Upper Velfreyan Substage, mid *gracilis* Biozone from 73m north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Berwyn Hills, Powys, Wales. 3. GLA HM AB1b latex cast of external mould of partial cranidium. 4. GLA HM AB 2b latex cast of ventral surface of cephalon showing pit elevation and enlargement of I1 to I3 arcs. 5., SM A6322, latex cast of ventral surface of cephalon note the vincular notches, all X5.



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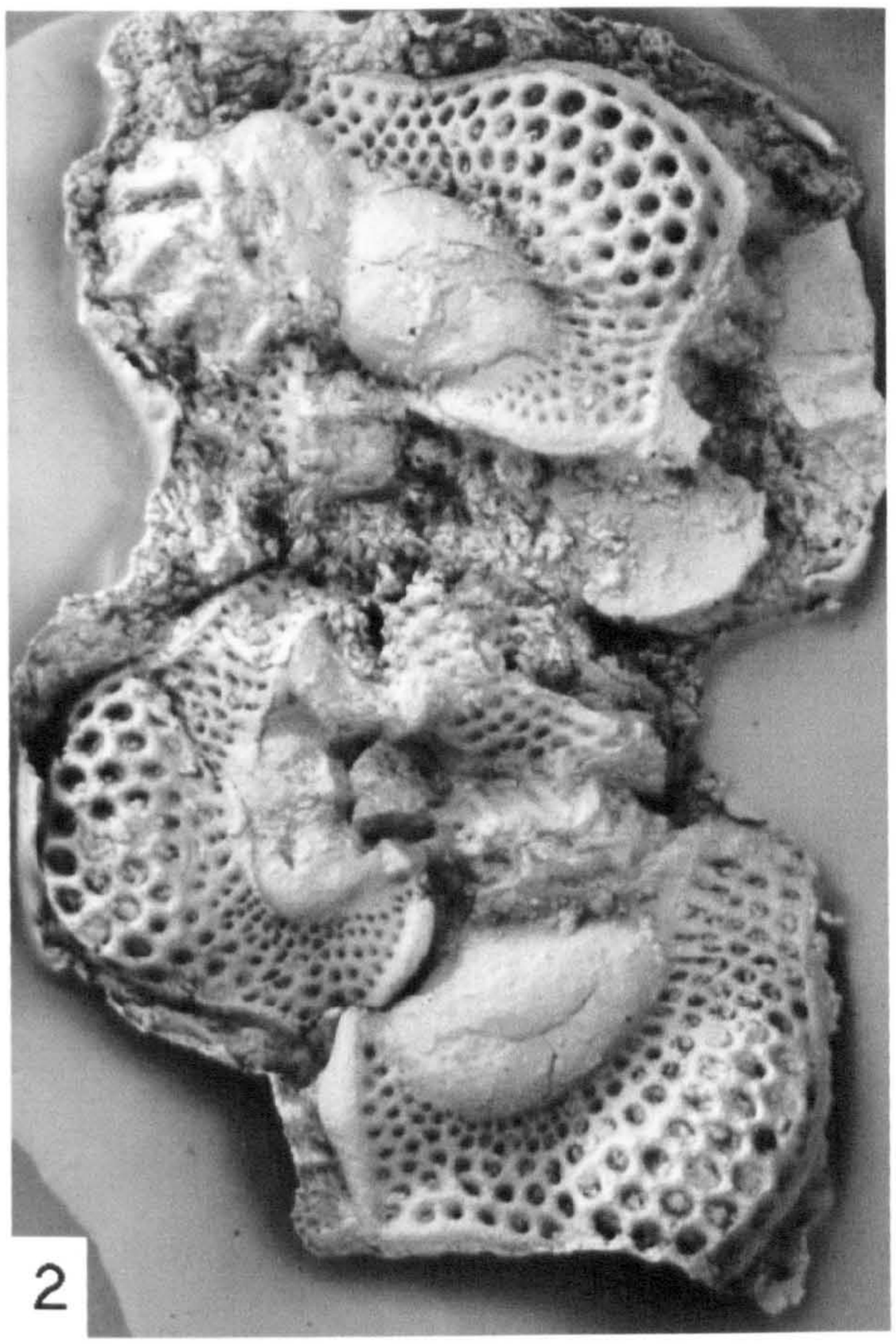

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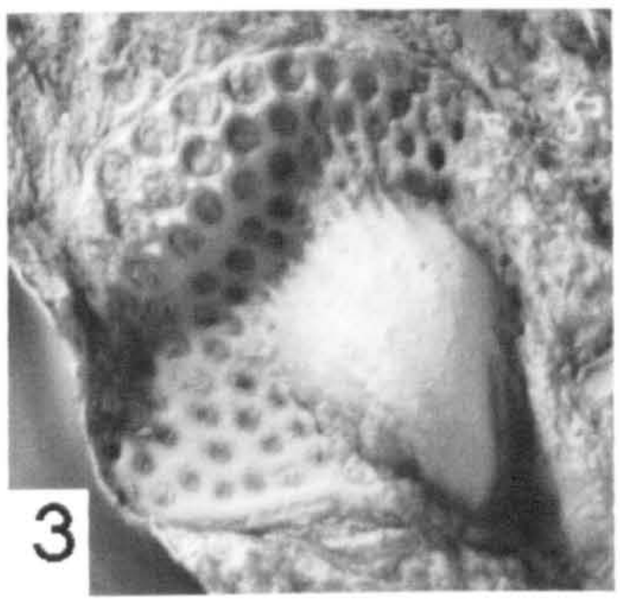

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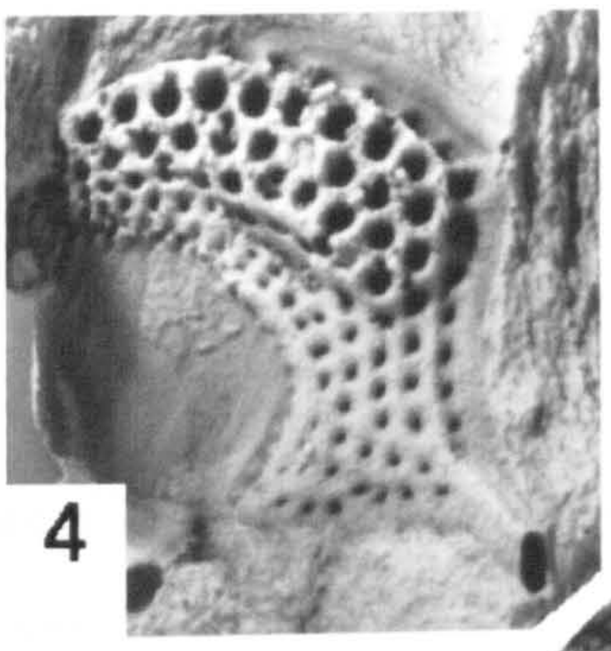

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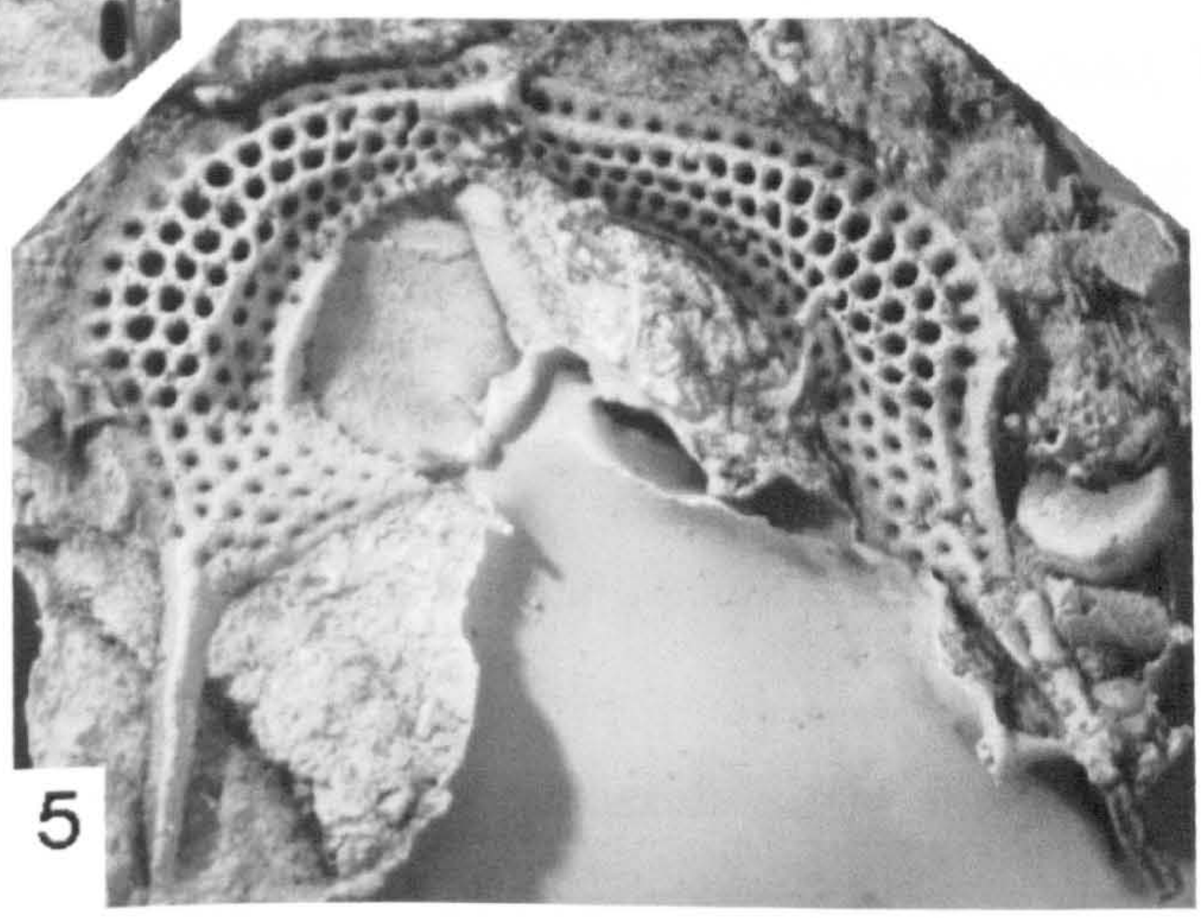

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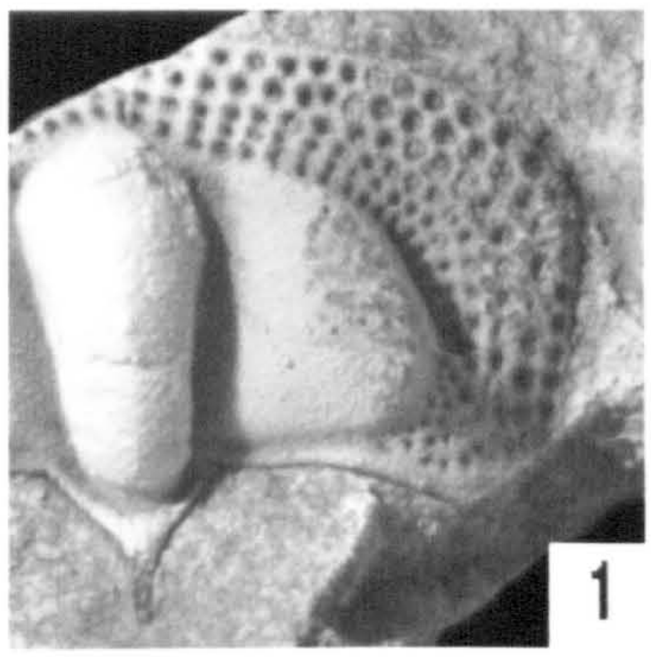
Explanation of Plate 3

Figs 1-4., *Marrolithus craticulatus* Whittard, 1956, 1., BIRUG 29021, internal mould of partial cranidium showing large pits in arcs E_1, I_1 and I_2. Meadowtown Formation, Upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Meadowtown Quarry, Shropshire, England, X5. 2., BGS 92999, paratype, latex cast of cranidium. From Betton Shale Formation, Lower Llanvirn Series, Upper Abereiddian Stage, upper *murchisoni* Biozone from the field south of the lane from Meadowtown to Castle Ring, Shelve, Shropshire, England, X5. 3., BIRUG 29022a, internal mould of ventral surface of lower lamella showing prominent girder frontally and developed first internal pseudogirder posterolaterally, note large E_1 arc pits. Same horizon and location as 1, X5. 4., BIRUG 29019a, internal mould of ventral surface of partial complete individual showing prominent girder frontally and large E_1 arc pits. Same horizon and location as 1, X5.

Figs 5-8., *Marrolithus* (sensu lato) *ultimus* Bancroft, 1949. 5. BNHM It 51708, latex cast from internal mould of partial cranidium, showing well organised pits to posterior region and I_1 and I_2 pits wider than others laterally with only slight inflation. From type locality Hoar Edge Formation (Coston Beds), Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone [= *Costonia ultima* beds] from old quarry 155 m south of Coston Farmhouse, Shropshire, England, X6. 6., BNHM In 52828, latex cast of external mould of partial cranidium showing low number of irregular pits posteriorly. From Hoar Edge Formation, Lower Caradoc Series, Aurelucian Stage, Costonian Substage, lower *foliaceus* Biozone from Gutter section, Bull Hill, Evenwood, Shropshire, England, X5. 7., BNHM Coston mark 21, latex cast of external mould of partial cranidium showing slight irregular pitting mesially. Same horizon and locality as 5, X5. 8., BNHM In 51703, Latex cast of ventral mould of lower lamella showing prominent braod girder frontally and elevated I_1 and I_2 pits posterolateraly note E_2 pits mesially. Same horizon and locality as 5, X5.



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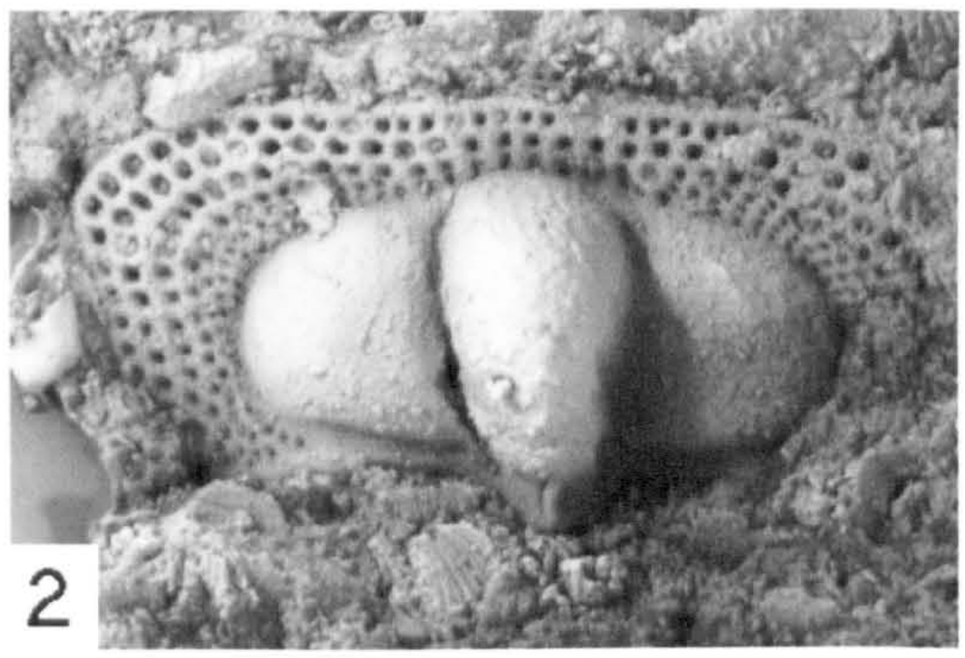

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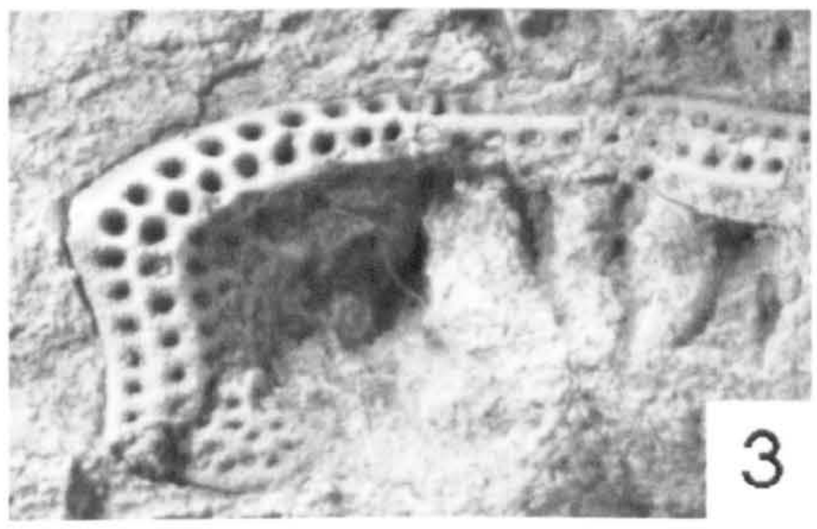

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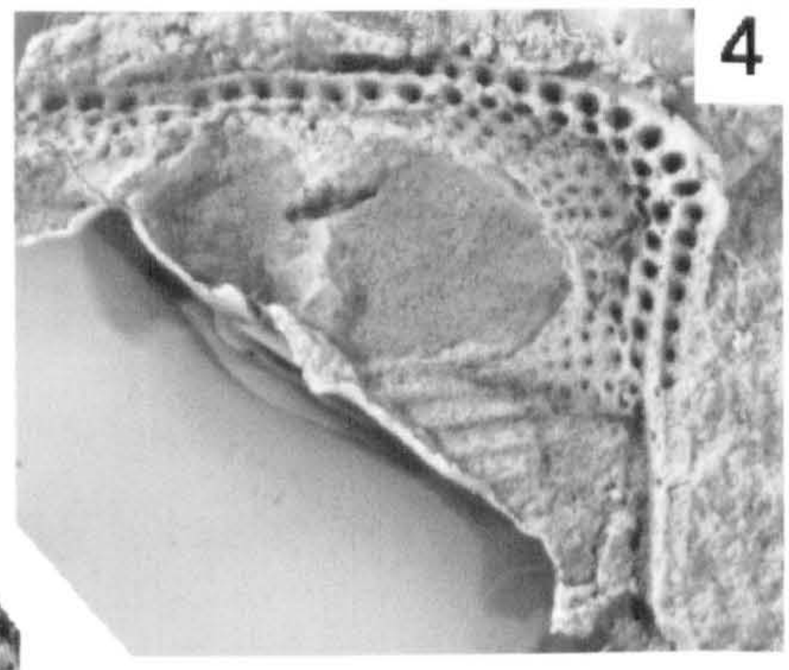

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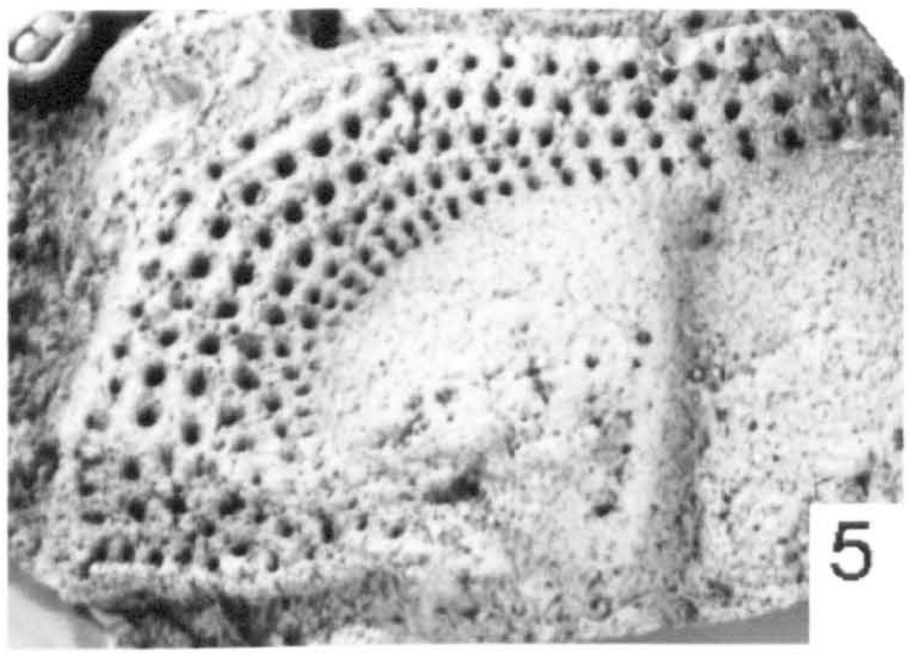

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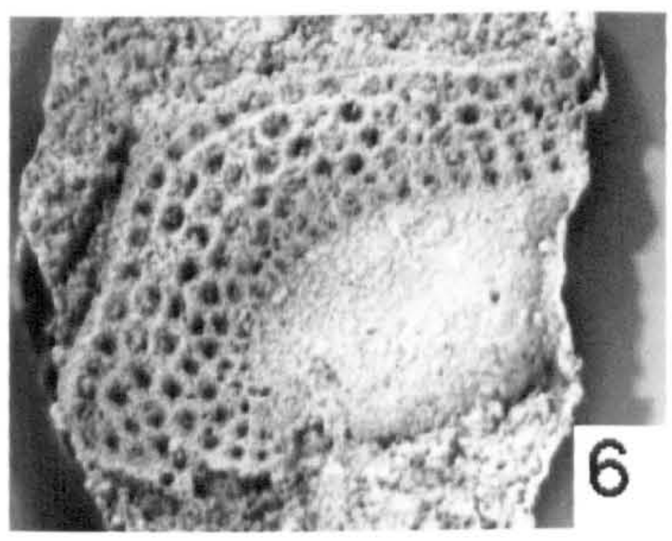

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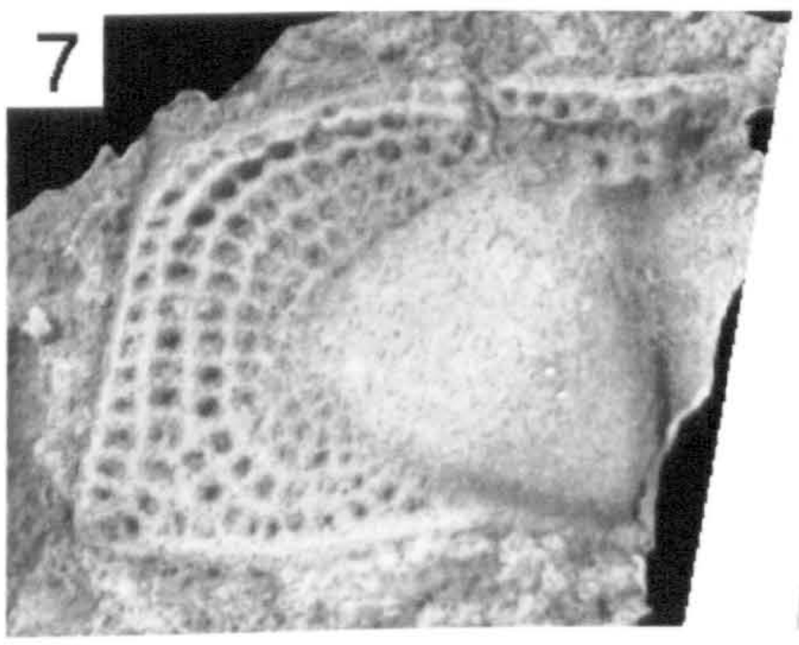

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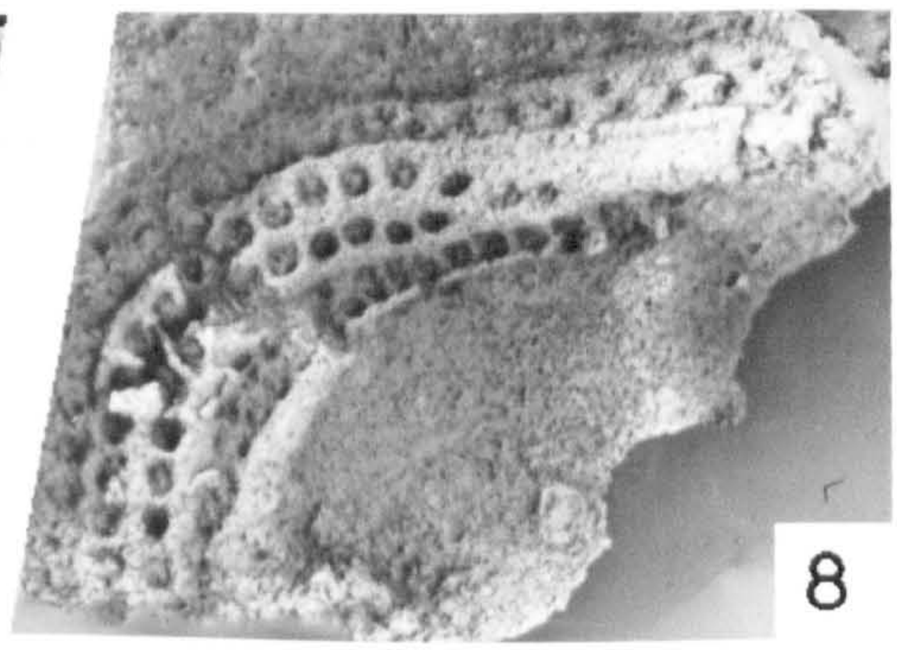

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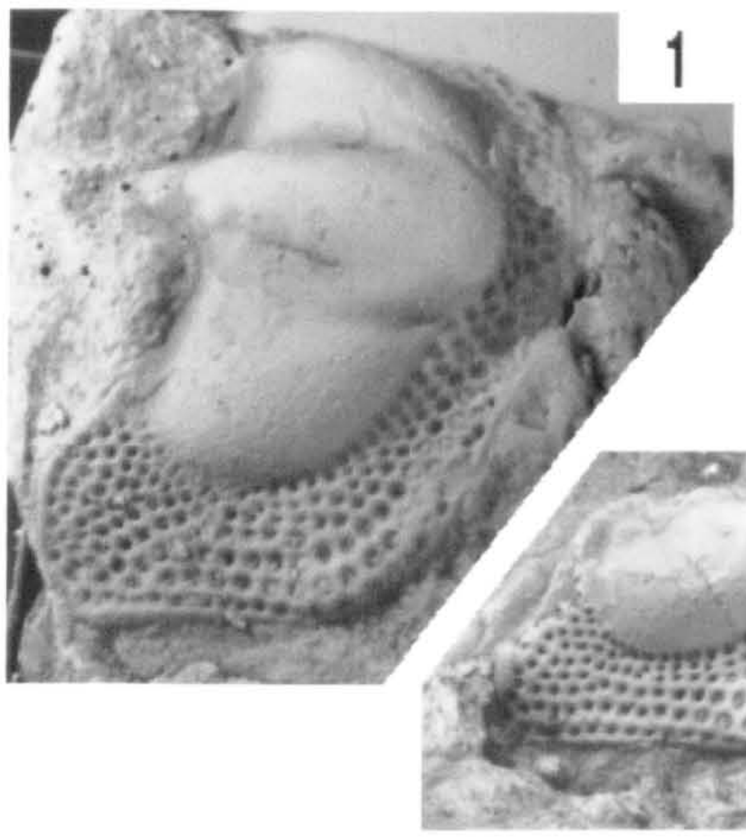
Explanation of Plate 4

Figs 1-11., *Marrolithus* (sensu lato) *elegans* (Dean, 1960), 1., BNHM In 49744 holotype, testiferous cranidium showing localized elevation of I_1 arc laterally note irregular E arc pitting frontally. From a limestone within the lower Hoar Edge Formation, *Harknessella subquadrata* Beds, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage from Round Nursery, 410m southeast of Harnage Grange, Shropshire, England, X5. 2., GLA HM AB3 internal mould of partial cranidium showing irregular E arc pits mesially. From the Hoar Edge Formation, *Harknessella subquadrata* Beds, Lower Caradoc Series, Upper Aurelucian Stage, Costonian Substage of quarry at east end of Black Dick's Coppice, Evenwood, Shropshire, England, X4. 3 –5., From the Bryn Banc Limestone Formation, lower Caradoc Series, upper Aurelucian Stage, Costonian Substage, Bryn Banc Quarry, Llan Mill, Pembrokeshire, SW Wales. 3., OUM B2950, partially testiferous cephalon showing localized I_1 elevation laterally and numerous small irregular pits posteriorly, note lack of extra E pits mesially, X3. 4., OUM B 2952, testiferous partial cranidium, X2. 5., OUM B 2446a, testiferous lower lamella showing elevated I_1 arc producing a "keel", note I_n cut off by I_3 and flange pits. 6-11., From the Bryn Banc Limestone Formation, lower Caradoc Series, upper Aurelucian Stage, Costonian Substage, 400 m north of Lower Court Farm, St. Clears, Dyfed 6, 9-10., BNHM It 10343, silicified partial cephalon showing low inflation on upper lamella and elevated I1 arc producing a "keel" on lower lamella, all X7. 7-8,11., BNHM It 10342, silicified partial cephalon showing low inflation on upper lamella and elevated I1 arc producing a "keel" on lower lamella, all X7.

Figs 12-14. *Marrolithus* (sensu lato) *arenarius* (Whittard, 1956). 12., BNHM It 10362a, damaged testiferous cranidium, showing slight lateral elevation of I1 arc and low number of irregular pits posteriorly allowing arc I_1 to extend to posterior margin. From Bryn Sion Sandstone Formation, lower Caradoc Series, Aurelucian Stage, *gracilis* Biozone from stream section in Cwm Llan Wood, 130m north of vicarage at Lampeter Velfrey, S. Wales, X3. 13., OUM B 2954, partially testiferous cranidium. From the Bryn Sion Sandstone Formation, lower Caradoc Series, Aurelucian Stage, Costonian Substage, Bryn Banc Quarry, Llan Mill, Pembrokeshire, SW Wales, X2. 14., OUM B 2953, testiferous lower lamella note the numerous elevated I_1 arc pits

and low number of irregular pits posteriorly. From Bryn Sion Sandstone Formation, Narberth Group, Lower Caradoc Series, Aurelucian Stage, *gracilis* Biozone from Stoneyford road section, Narberth, Pembrokeshire, S. Wales, X3.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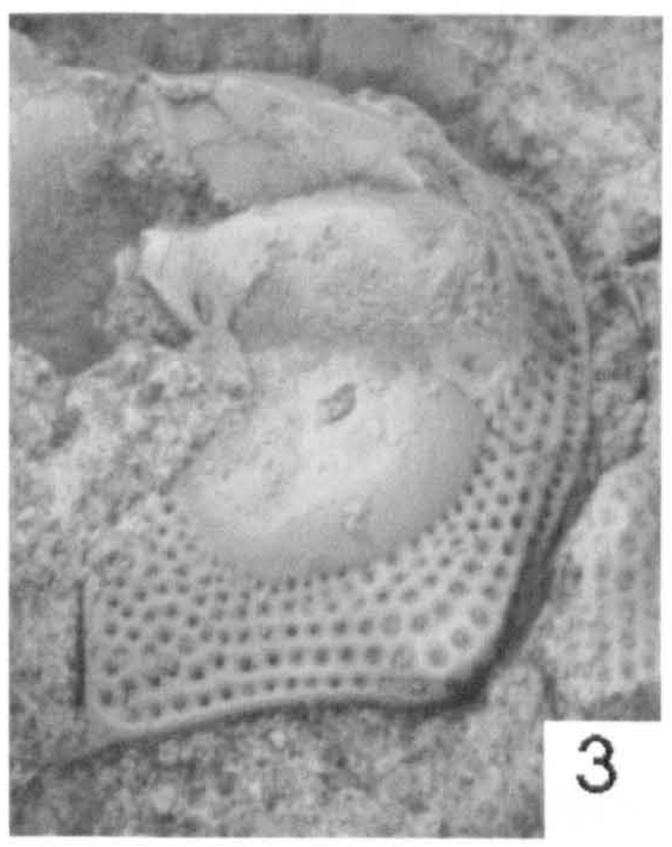
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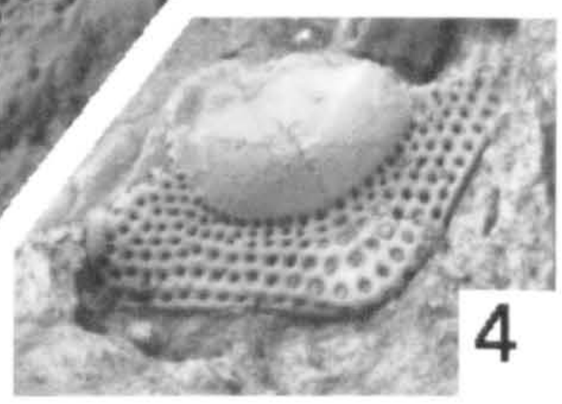
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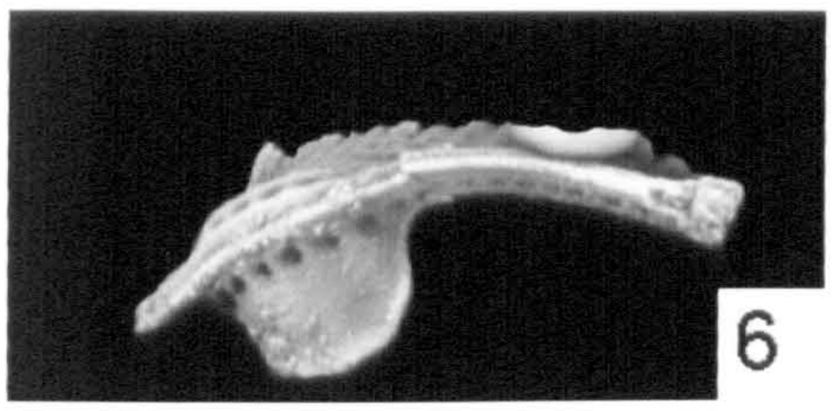
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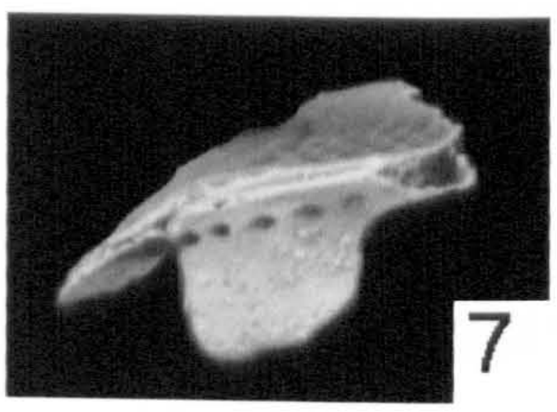
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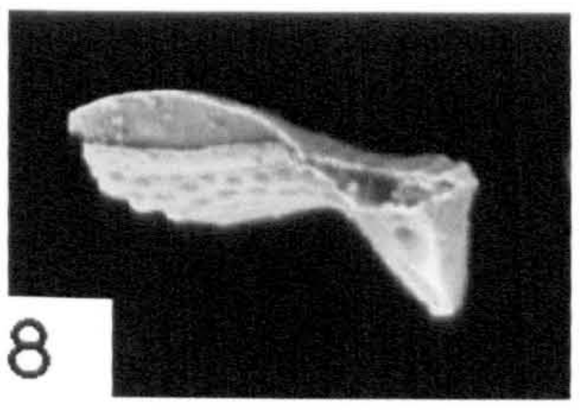
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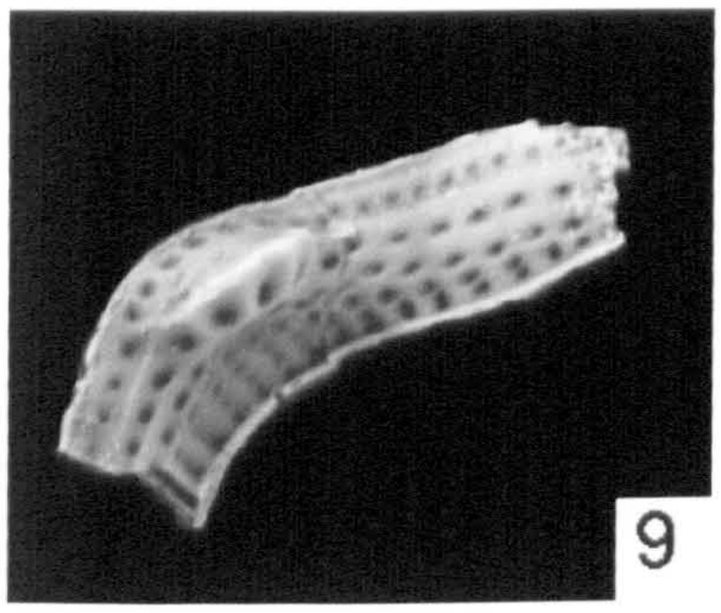
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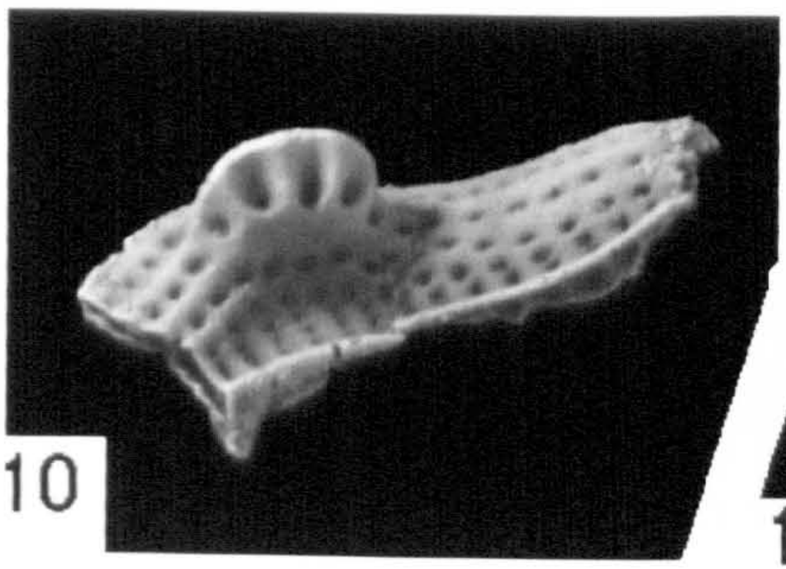
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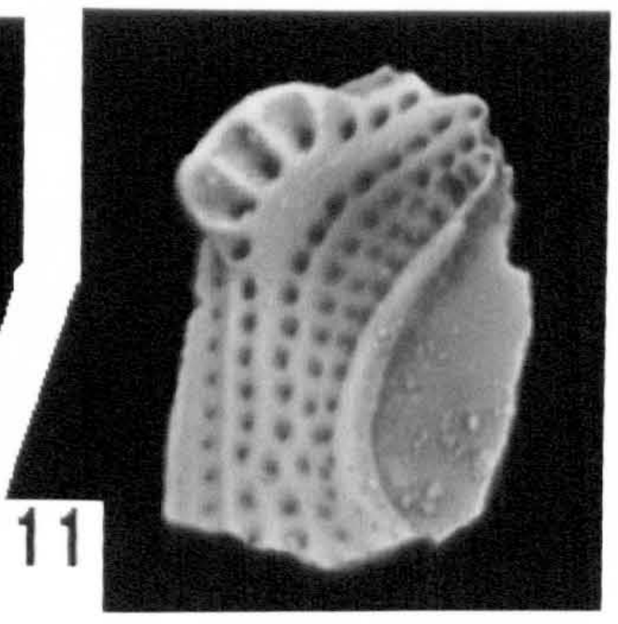
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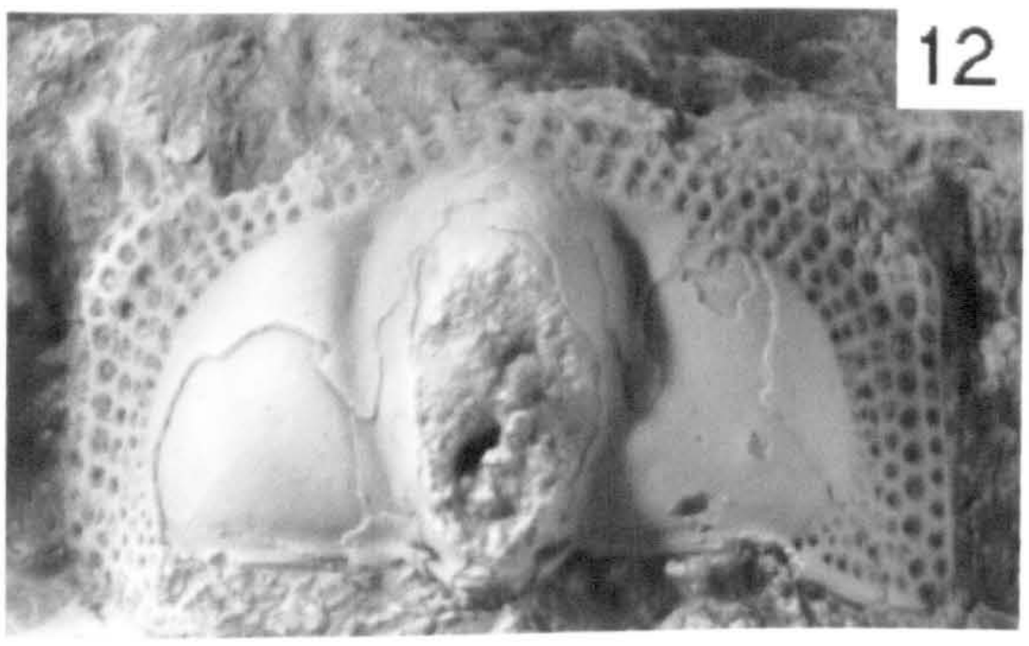
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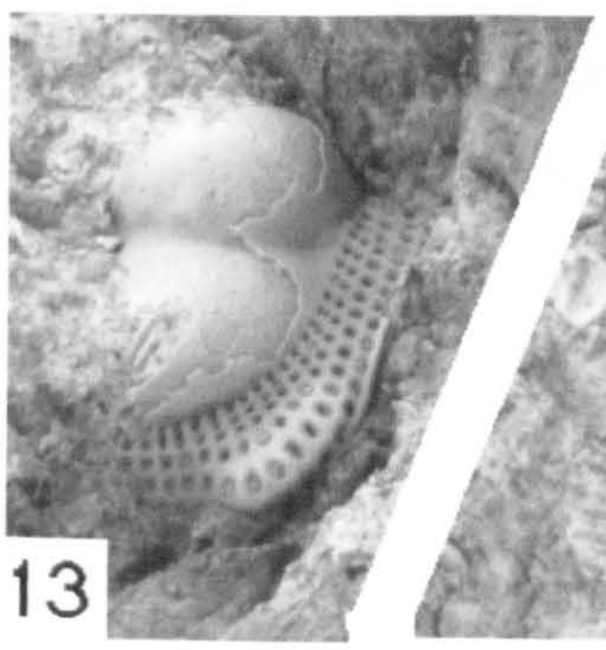
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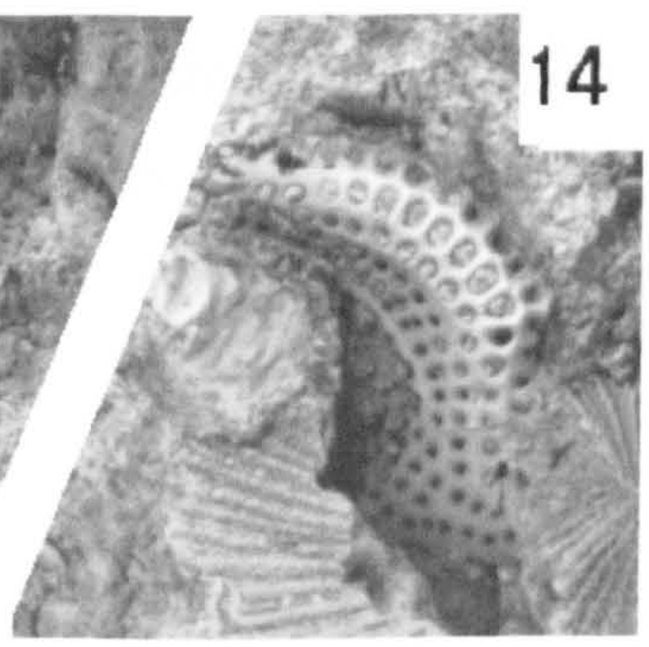
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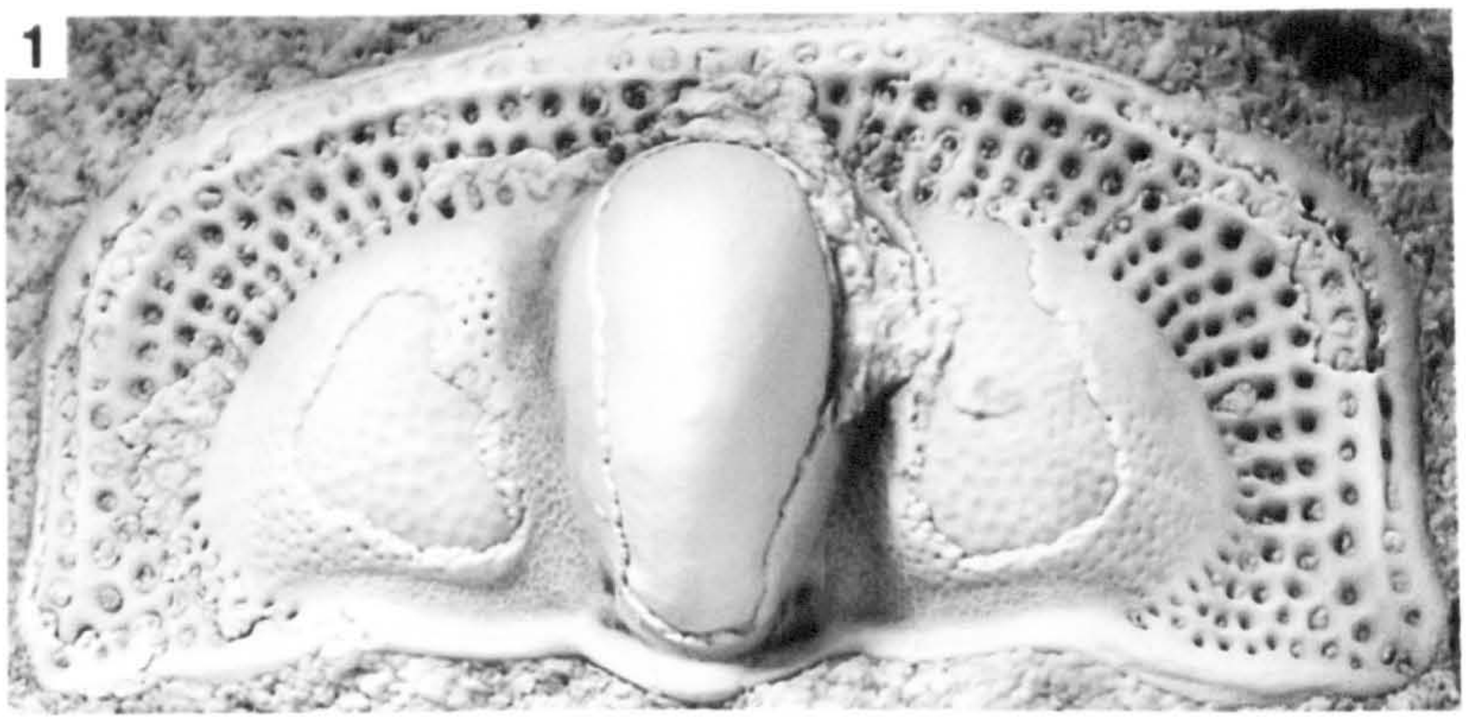
Explanation of Plate 5

Figs 1-8. *Hammannaspis ornata* (Sternberg, 1833), gen. nov., all from the Zahořany Formation, upper middle Caradoc Series (approximately upper Cheneyan Stage – lowest Streffordian Stage), Loděnice road cutting, Prague Basin, Czech Republic. 1., BNHM It15850a/1a, partially testiferous cranidium showing faint genal caeca and slightly elevated I_1 arc anterolaterally. Note lack of occipital spine, X10. 2., detail of same specimen, showing the contrast between the pronounced pitting of the genal lobe and the delicate reticulate sculpture of the axial furrows, X20. 3., BNHM It15850b/7. latex peel from external mould of damaged cranidium showing fringe features well, including prominent girder list, slightly elevated I1 arc anterolaterally and outwardly declined E_1 arc, X6. 4., BNHM It15850a/2a, immature, probably meraspid, largely testiferous cranidium, showing pronounced ocular ridges across axial furrows, well-developed baculae, little trace of I_1 elevations anterolaterally and incomplete I arc development adjacent to I_n, X20. 5., BNHM It 15850a/8, latex cast from external mould of partial lower lamella, showing girder, particularly pronounced mesially and well-developed first internal pseudogirder laterally, X6. 6., BNHM It15850b/5b, internal mould of pygidium and last thoracic segment, X10. 7., BNHM It 15850b/4b, latex cast of external mould of pygidium, showing fine reticulate sculpture on anterior pleural band of each pygidial segment, X10. 8., UUG JV1403, internal mould of partial cranidium, figured by Čech (1975, pl. 2, fig. 4 [as *Marrolithus ornatus ornatus*]), showing well-defined spiculate areas (?muscle attachment zones) anterior to axial furrow and along lateral margin of genal lobe – also noted in the marrolithine *Onnia ultima* [= *superba*] subspp. by Owen and Ingham (1988, pp. 842, 846, text-fig. 7G) and a short development of I5 anterolaterally, X22.5.

Figs 9-12. *Hammannaspis novaresei* (Hammann and Leone, 1997), gen. nov., the type species, all from the Portixeddu Formation, horizon Th3a (supposedly Ashgill Series, Pusgillian Stage but possibly slightly older, "Ovile Cannamenda", SE of Bacu Abis, Iglesiente-Sulcis autochthon, southern Sardinia, figured by Hammann and Leone (1997, pl. 27, figs 1d, 2a-c [as *Deanaspis ? novaresei* sp. nov.]). 9-11., IPUM 52133, holotype, internal mould of cranidium, showing pronounced girder list, outwardly declined E_1 arc with high pit count, little or no elevation of I_1 anterolaterally and

absence of occipital spine, X5. 12., IPUM 52132, paratype, latex cast of partial ventral surface of lower lamella, showing pronounced girder throughout and less well-defined first internal pseudogirder laterally, X7.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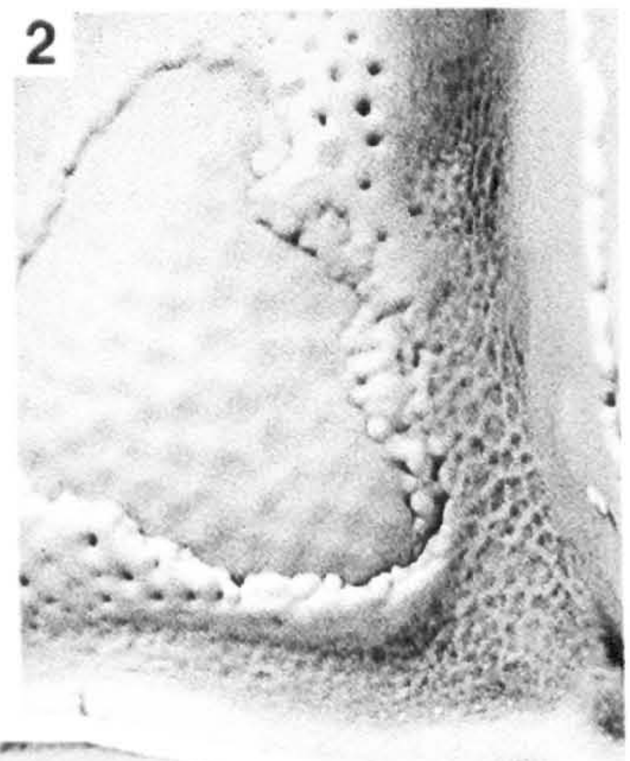
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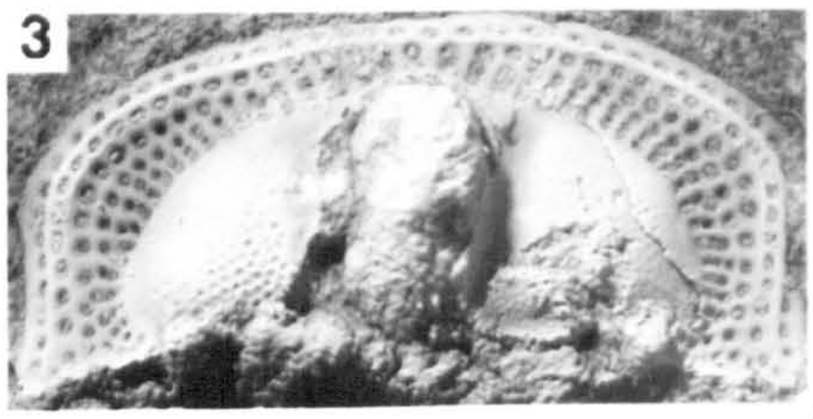
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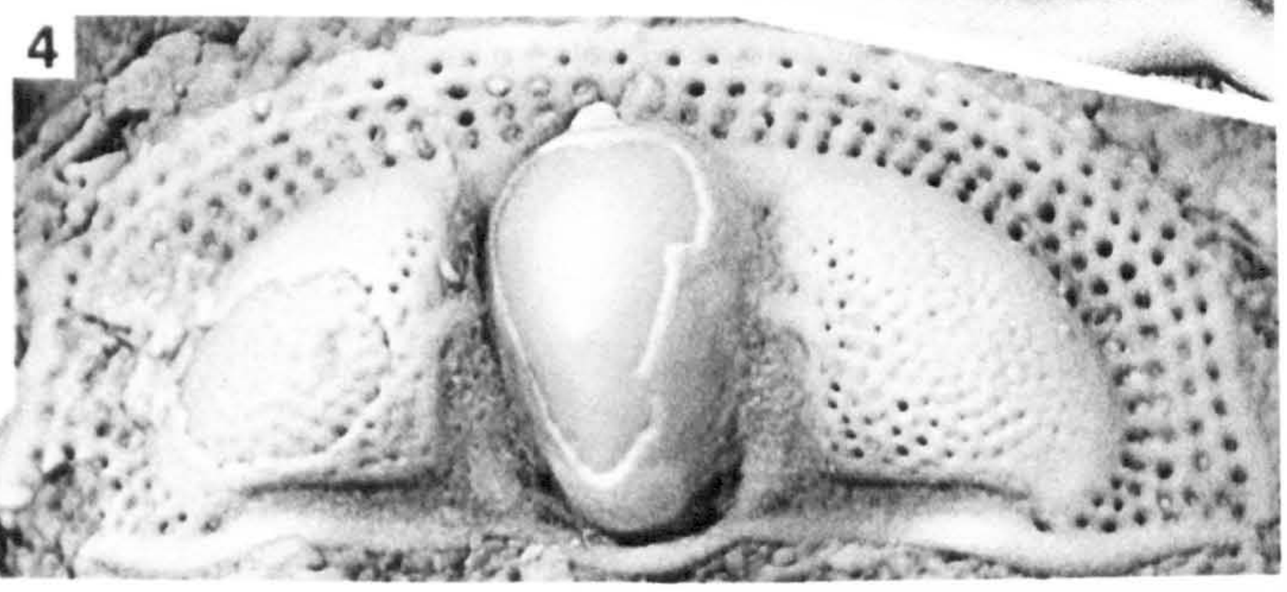
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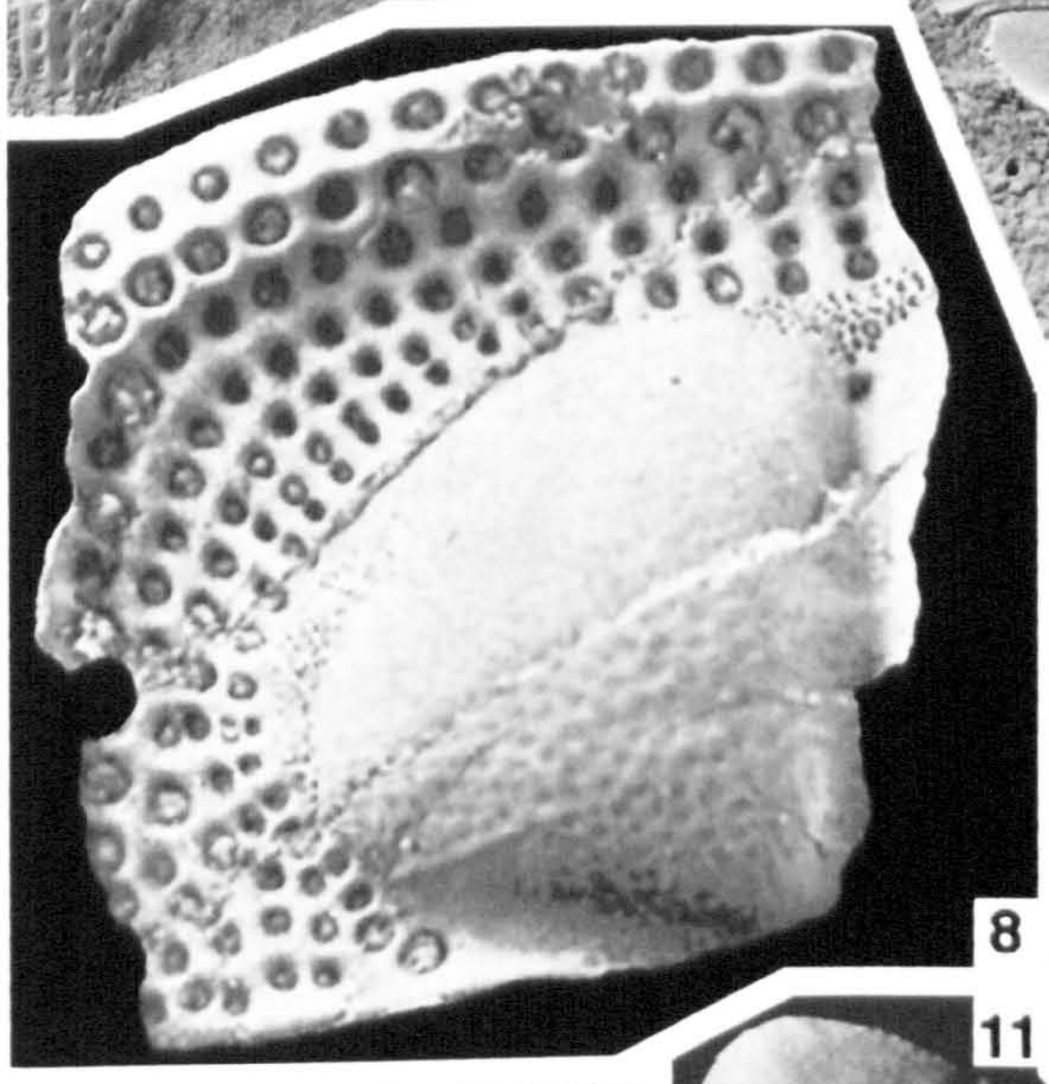
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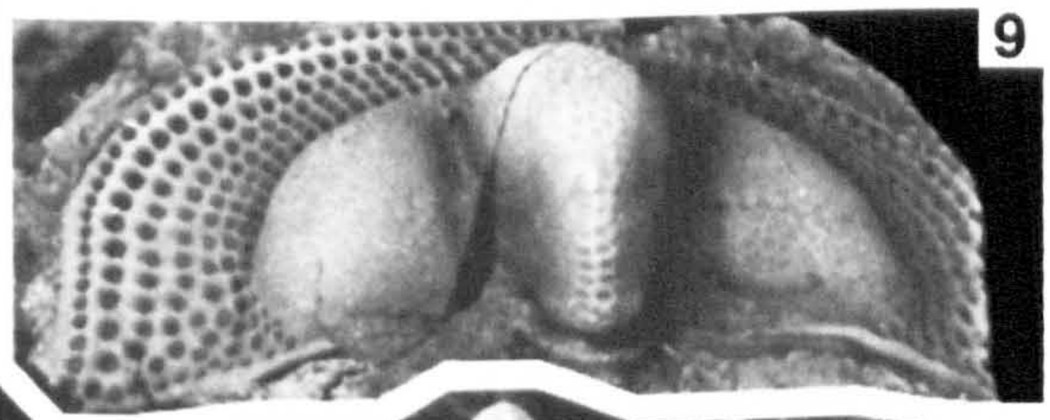
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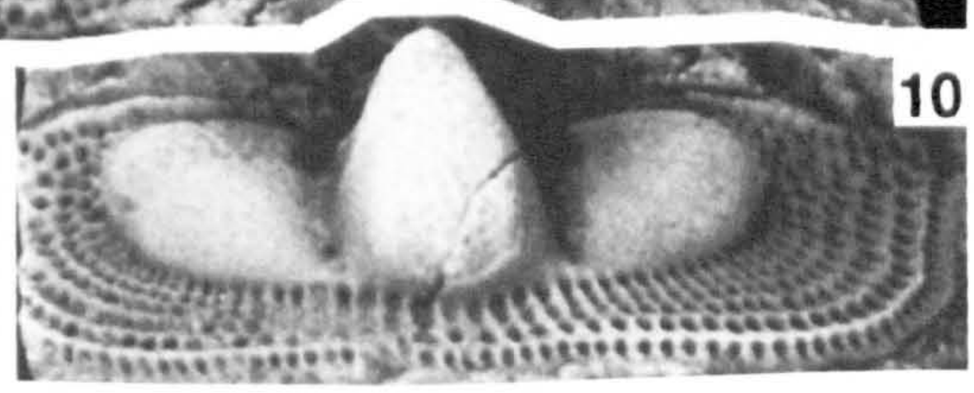
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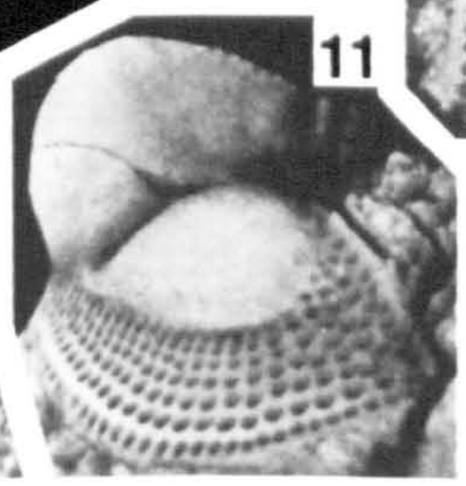
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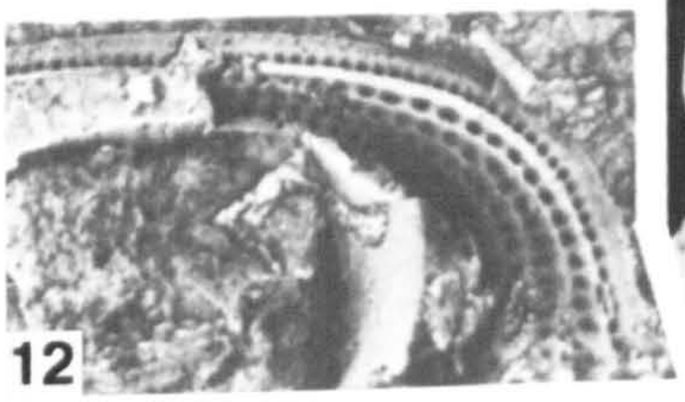
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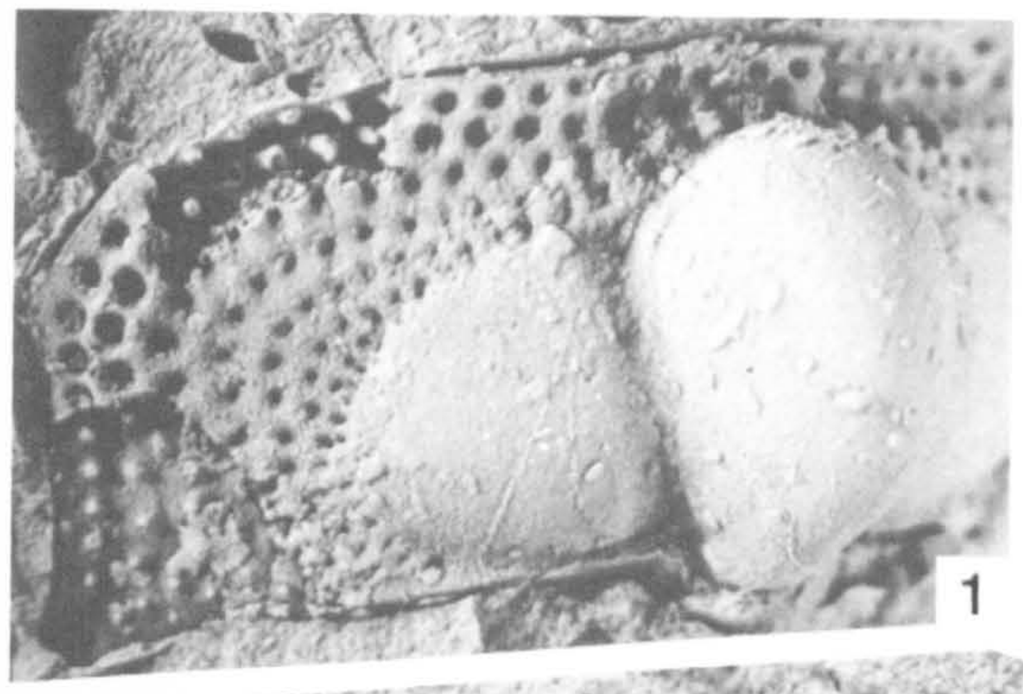
Explanation of Plate 6

Figs 1, 2. *Hammannaspis? paulisper* (Přibyl and Vaněk, 1969), gen. nov., both from the Nučice Ore Unit at the base of the Vinice Formation, Middle Caradoc Series, at the former Chrustenice Mine, Chrustenice, Prague Basin, Czech Republic. 1., UUG JV 953, holotype, internal mould of cephalon exposing partial ventral mould of lower lamella showing the first internal pseudogirder (upper right) is well-developed frontally and is more marked than the girder there. Note the fringe invagination behind the anterolateral angulation of the fringe margin, the slight elevation of the I_1 arc anterolaterally and the total absence of sculpture impressions on the internal moulds of glabella and genal lobes, X4. 2., CNM L 30795, internal mould of damaged cephalon, showing ventral mould of part of the lower lamella. Note the stout occipital spine and the "spicular" zones at the end of the axial furrow and near the lateral margin of the genal lobe, X5.5.

Figs 3-11. *Hammannaspis prima* gen. et sp. nov., all from either the topmost beds of the Izgouiren Sandstone Formation of the First Bani Sandstone Group, Llanvirn Series, upper Llandeilian Stage, or the bottom of the Lower Tiouririne Sandstone Member of the Lower Ktaoua Formation, Ktaoua Clay/Sandstone Group, basal Caradoc Series, from Jbel Hajra el Beida, near Taouz, Tafilalt District, Anti Atlas Mountains, southern Morocco, Grid Ref. 606.2/457.3. 3., MGS 1484/3, imperfect holotype testiferous cephalon, showing much of upper lamella ventral impression of part of lower lamella. Note distinct girder list, outwardly declined E_1 arc and elevated I_1 arc anterolaterally, X5. 4., MGS 1484/8, partially testiferous paratype cranidium, showing distinctive sculpture even on internal mould, closely comparable with that of the much younger *H. novaresei* (see Pl. 5). Note short occipital spine, X10. 5., MGS1484/10, partially testiferous, incomplete cranidium, X10. 6., MGS 1484/7, largely testiferous, partial paratype cranidium, showing faint genal caecum, X10. 7., MGS 1484/5, fragment of upper lamella, showing sharply elevated I_1 arc, X5. 8., MGS 1484/6, partial paratype cephalon, showing ventral view of testiferous lower lamella. Note prominent girder frontally and weak first internal pseudogirder anterolaterally, X5. 9., MGS 1484/1, partial cephalon, showing part of testiferous lower lamella, X5. 10., MGS 1484/4, part of testiferous lower lamella, X5. 11., MGS 1484/2, almost complete, largely testiferous paratype pygidium, showing fine

reticulate sculpture on anterior pleural bands. Compare with that seen on the pygidium of the younger *H. ornata* (see Pl. 5), X10.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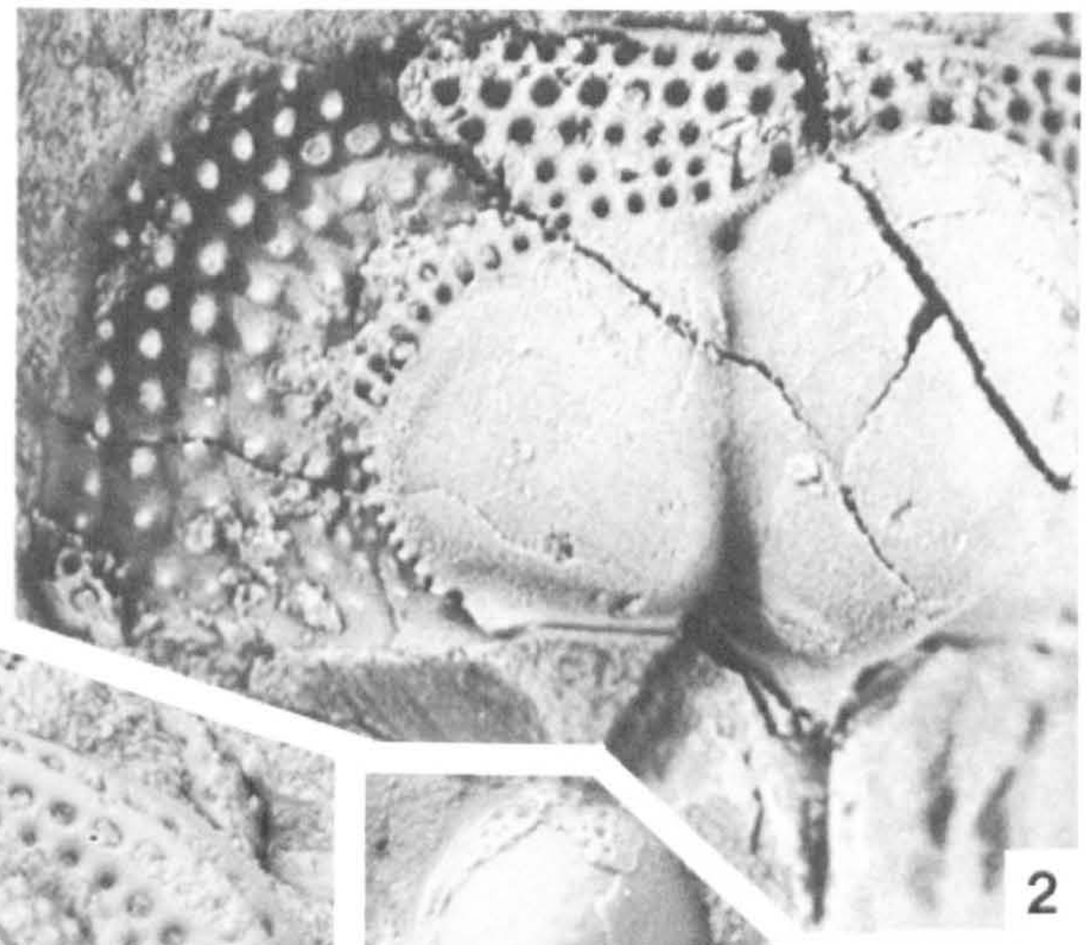
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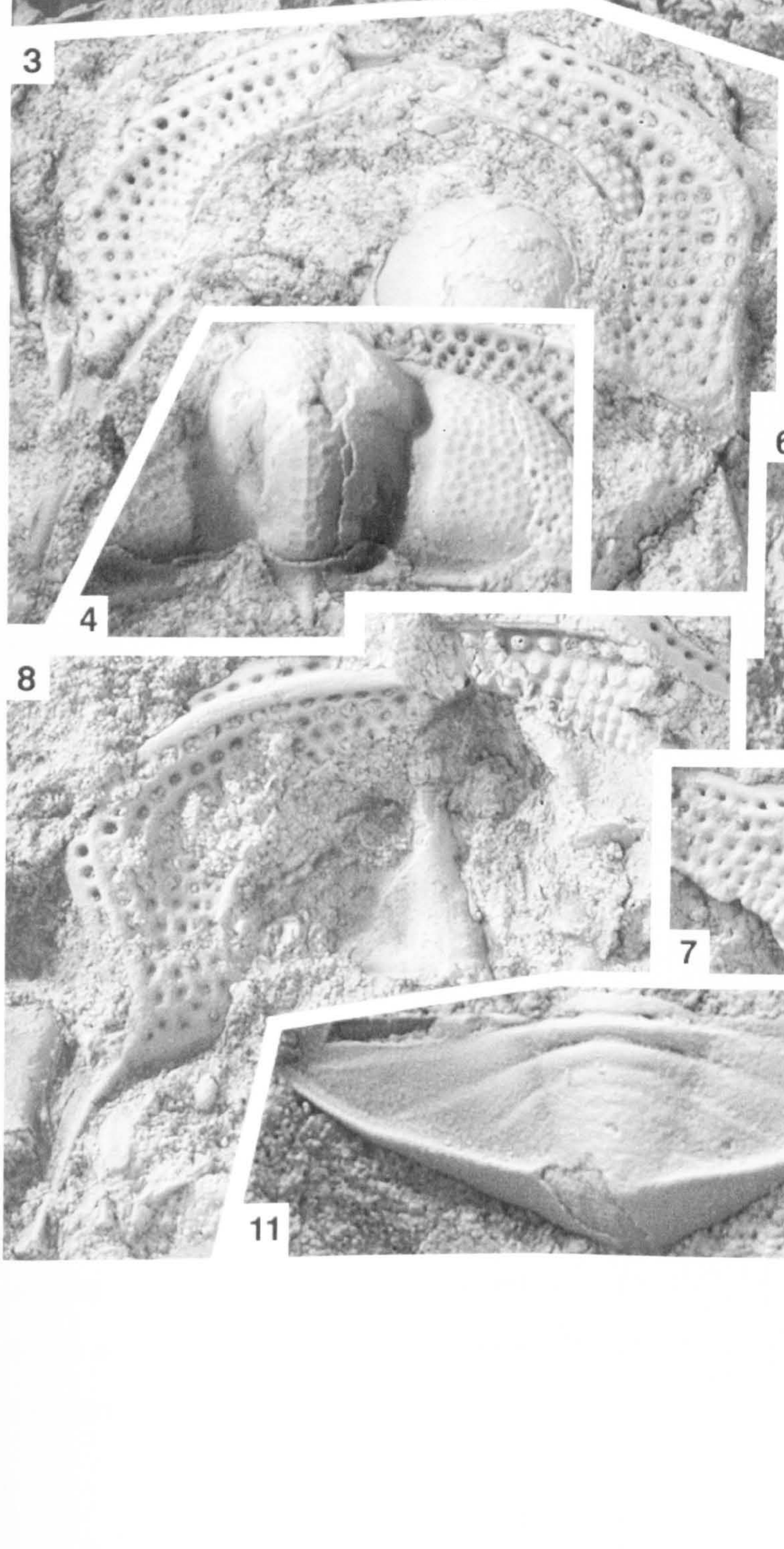
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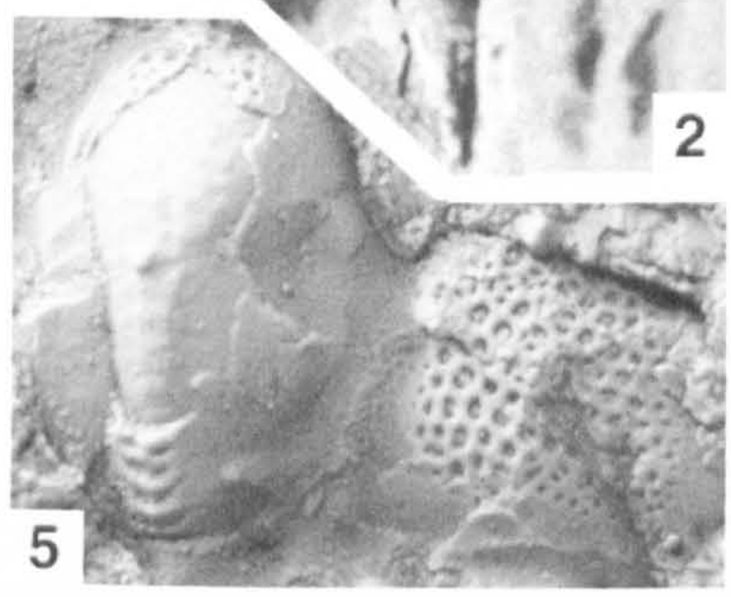
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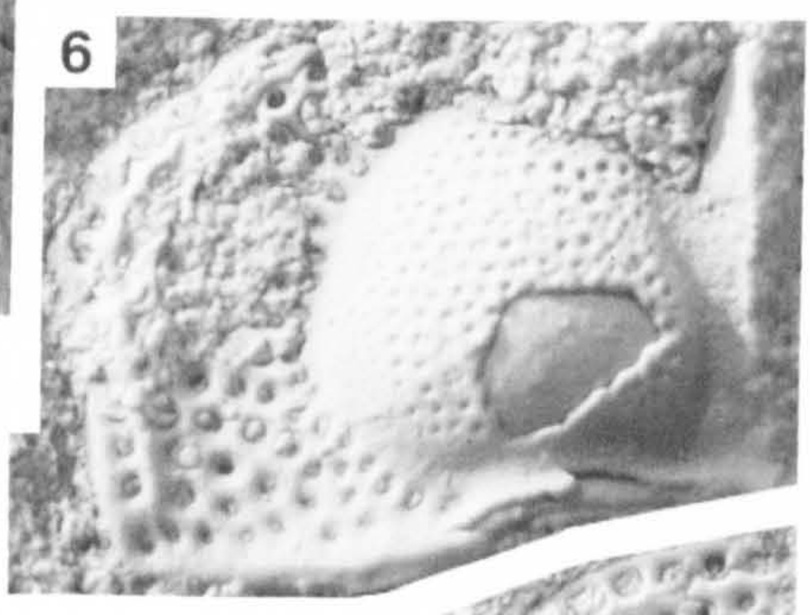
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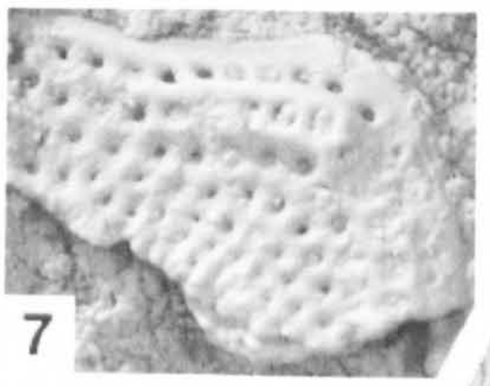
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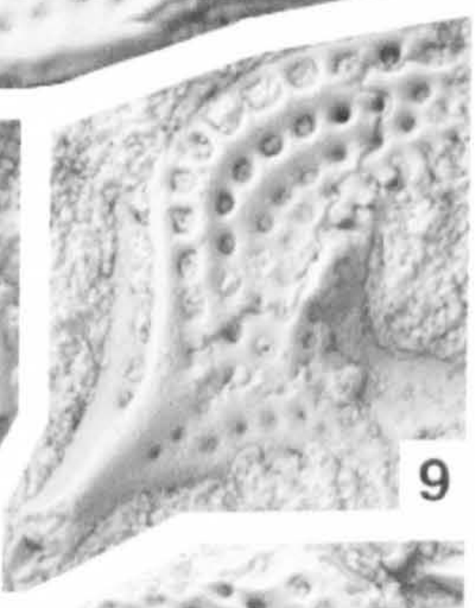
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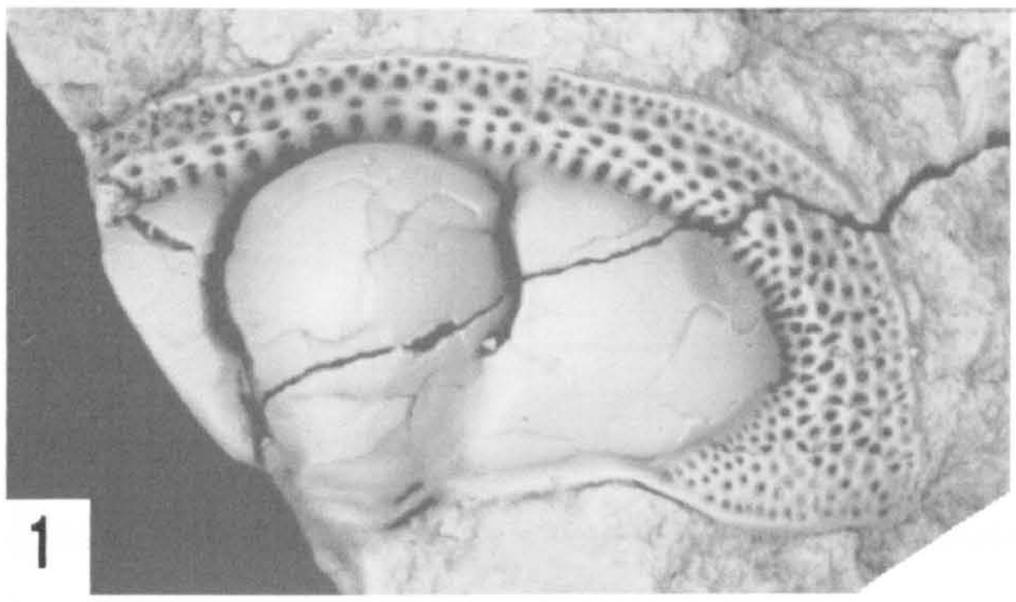
Explanation of Plate 7

Figs 1,3-7. *Reuscholithus reuschi* Bancroft, 1929b, from the lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, lower Harnagian Substage, *Reuscholithus reuschi* and *Salterolithus harnagensis* local Biozone, *foliaceus* Biozone of the north bank, 65m below weir, Coundmoor Brook, Shropshire, England. 1., GLA HMA11948a, internal mould of partial cranidium, X4. 3., GLA HMA 11941, internal mould of partial cranidium, X4. 4, GLA HMA10956a, internal mould of meraspid stage cranidium showing faint genal caeca, X6. 5., GLA HMA10946, internal mould of possible meraspid stage cranidium showing faint genal caeca, note genal prolongation is not evident, X5. 6., GLA HMA1095/7, testiferous lower lamella showing prominent girder frontally, X3. 7., GLA HMA11008a, internal mould of ventral surface of lower lamella showing prominent girder frontally, X5. 2., BNHM In42080, holotype, latex cast of internal mould of cranidium. From the lower Harnage Shale Formation, Smeathen Wood Member, Caradoc Series, Burrellian Stage, lower Harnagian Substage, *Reuscholithus reuschi* and *Salterolithus harnagensis* local Biozone, *foliaceus* Biozone from the trackway outside the southeastern corner of Smeathen Wood, Horderley, Shropshire, X5.

Figs 8-12. *Bettonolithus chamberlaini* (Elles, 1940), 8. GSM 86787, latex cast of external mould of cephalon, previously figured by Whittard (1956, pl. 9, fig 9 [= *B. paucipuncta* Whittard, 1956]). From the Upper Camnant Mudstones Formation, lower Llanvirn, lower Abereiddian, lower *murchisoni* Biozone [= *D. speciosus* Subzone of Elles 1940] from the cliff section, Howey Brook, Carregwiber, Llandrindod Wells, Powys, Wales, X8. 9., NMW 91.47G.23a, partially testiferous specimen showing E_2 pits frontally. From Builth Volcanic Formation, middle Llanvirn, upper Abereiddian, mid *murchisoni* Biozone, small excavation on low hill 200m from Maen Cowyn, 1.25km NE of Llanelwedd Church, Powys, X5. 10., NMW 95.22G.102c, latex cast of internal mould of pygidium. Same horizon and location as 8, X5. 11., NMW 85.2G.158a, internal mould of cranidium note E_2 pits frontally. Same horizon and location as 8, X5. 12., NMW 91.47G.47, external mould of ventral surafce of lower lamella showing distinct girder and first internal pseudogirder along entire fringe as in *Deanaspis* species, note no E_2 pits frontally. Same horizon and location as 9, X5.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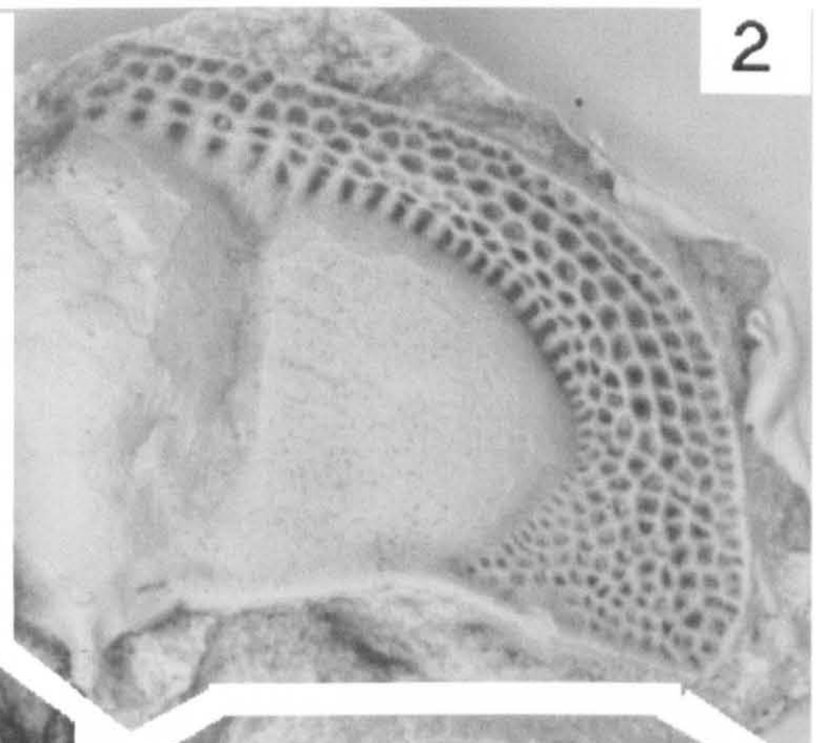
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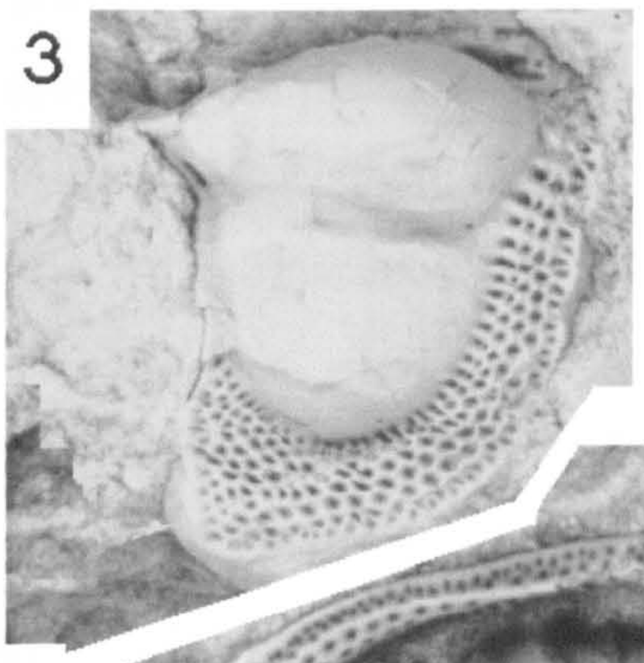
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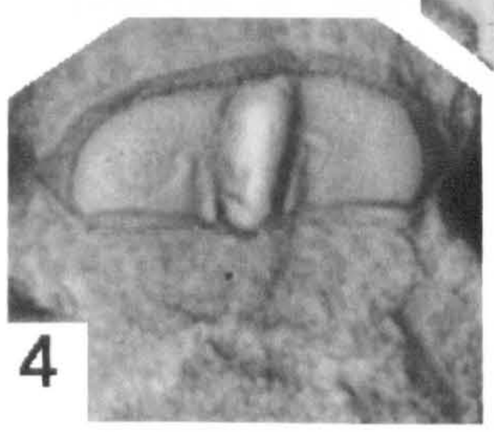
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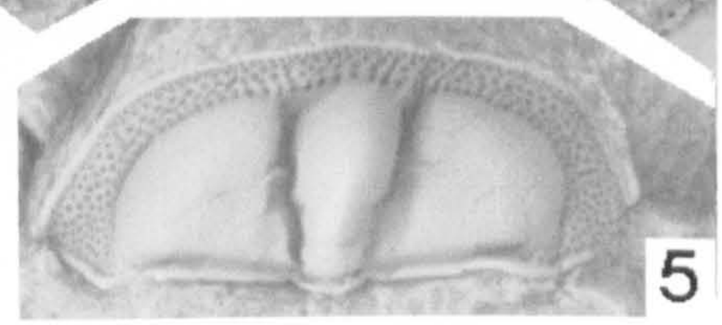
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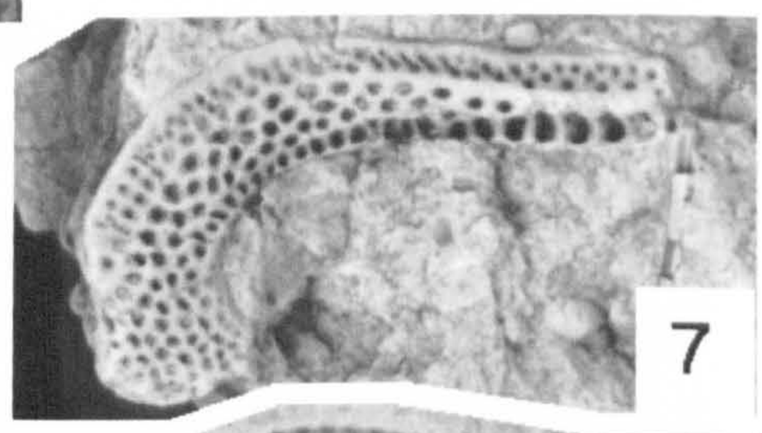
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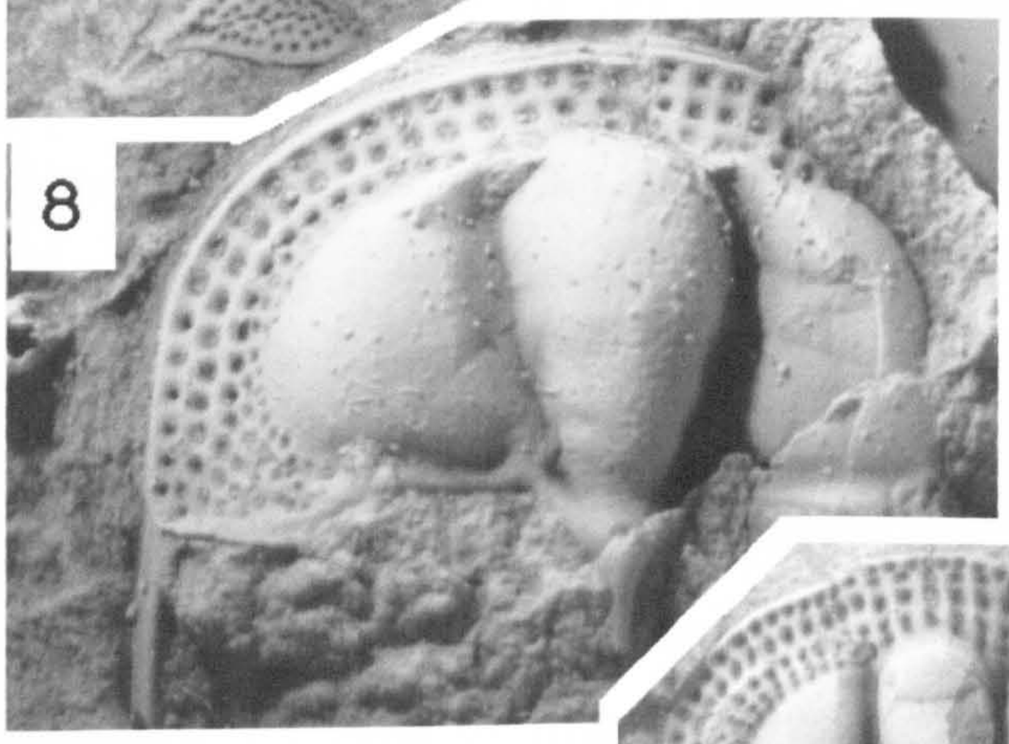
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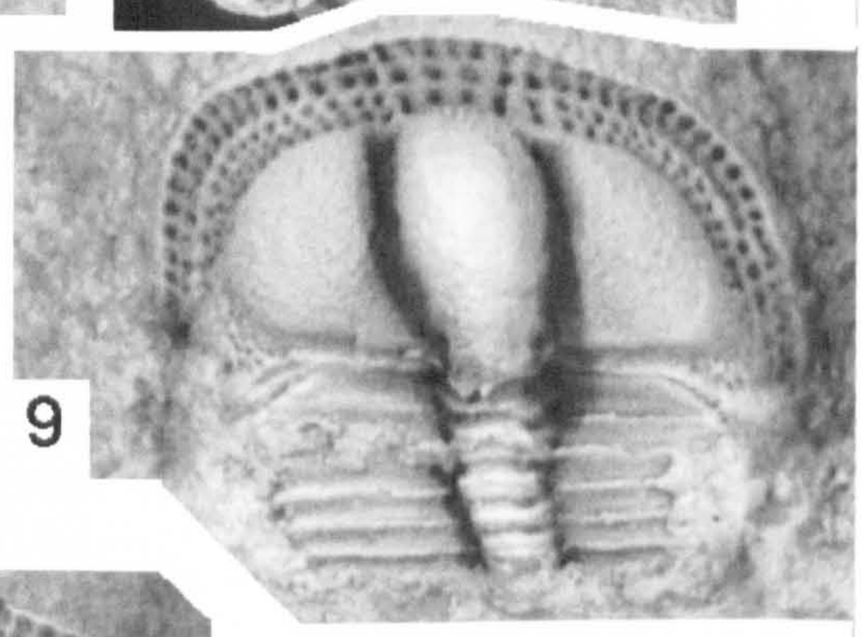
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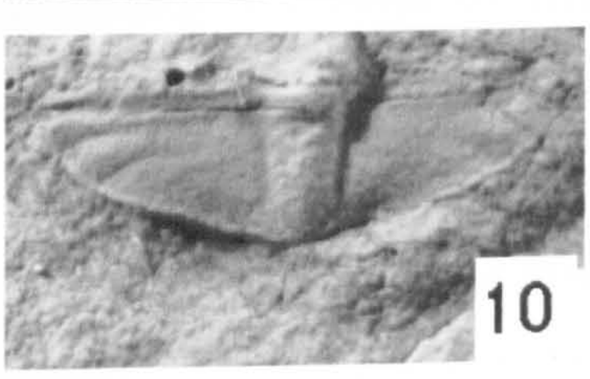
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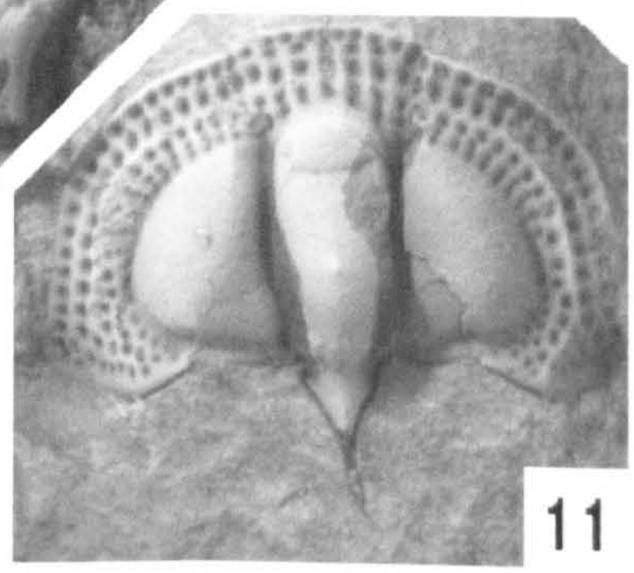
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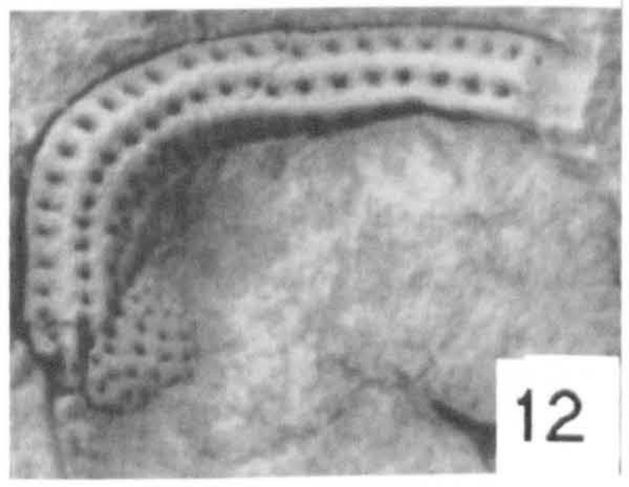
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Explanation of Plate 8

Figs 1-3. *Lloydolithus lloydi* (Murchison, 1839), 1., BNHM It 10370, latex cast of ventral surface of cephalon showing distinct girder and E_2 arc, figured by Whittard (1958, pl. 11, fig. 10). Meadowtown Formation, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from road cutting between Meadowtown and Rorrington, Shropshire, England, X3. 2., BIRUG 209016, latex cast of external mould of nearly complete individual. From Meadowtown Formation, Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone from Betton Quarry, Betton Wood Farm, Meadowtown, Shropshire, England, X5. 3., BMHM It 10370, latex cast of partial cranidium showing the posterior region of extensive small irregular pits. From Hendre Shale Formation, Llanvirn Series, Llandeilian Stage 847m west of Ty-newydd Farm, Methyr, Carmarthenshire.

Figs 4-10., *Whittardolithus superstes* (Whittard, 1958). 4., BNHM In 4341, latex cast of partial cranidium showing E_2 frontally and irregular pits posteriorly. From the lower Llanfawr Mudstone Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone, Wellfield Lodge, Builth district, Wales, X2. 5., BNHM It 10378, internal mould of two partial cranidia. Lower Llandeilo Flags Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone, south bank of road cutting Llangadock to Ffairfâch road, Llandeilo, Wales, X3. 6., BGS 86799a, latex cast of nearly complete individual, figured by Whittard (1958, pl. 10, fig. 8 [= holotype of *W. intertextus* (Whittard, 1968)]. From Betton Shale Formation, Llanvirn Series, upper Abereiddian Stage, upper *murchisoni* Biozone of bank in tributary of Lower Wood Brook, 265 m N of White House, Meadowtown, Shropshire, England, X3. 7., BNHM It 10380, internal mould of partial cranidium showing F pits extending forwards to row 9. From lowermost Hendre Shale Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone at north corner of Wood in Pant-yr-Hendre quarry, Meirdrim, S. Wales, X6. 8. GLA HM AB 4, partial internal mould of individual and dorsal surface of lower lamella. From **** , X3. 9., BNHM It 10377, latex cast of external mould of partial cranidium. Same horizon and location as 7, X3. 10., BNHM It 2793, latex cast of ventral surface of lower lamella showing distinct girder and developed frist internal pseudogirder, figured by Hughes (1971, pl. 9, fig. 4 [= paratype of *W. instabilis* (Hughes, 1971)]. From Lower Llanfawr

Mudstone Formation, upper Llanvirn Series, Llandeilian Stage, *teretiusculus* Biozone of stream bank in Dulas Brook, 138 m southwest of Maesgwynne, Builth Wells, Wales, X5.


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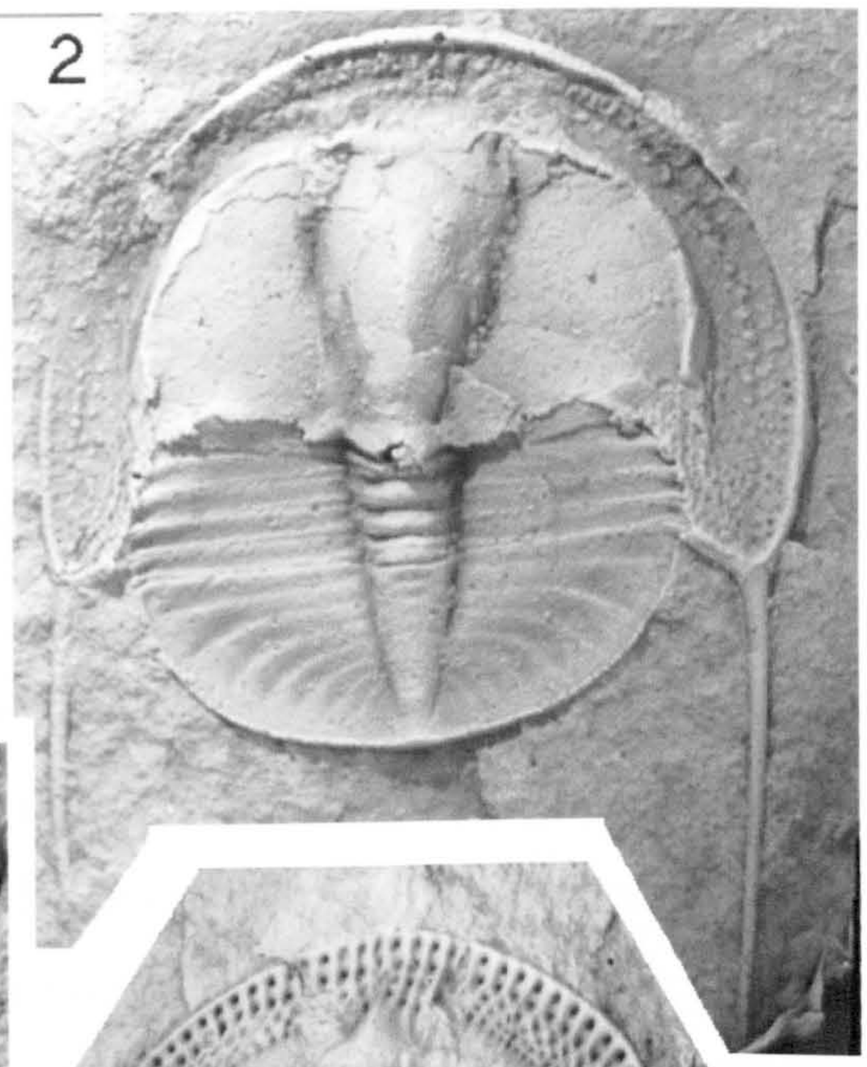
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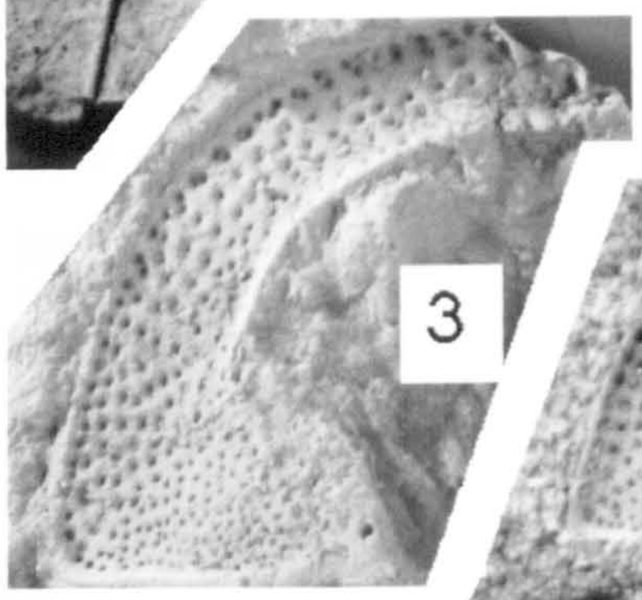
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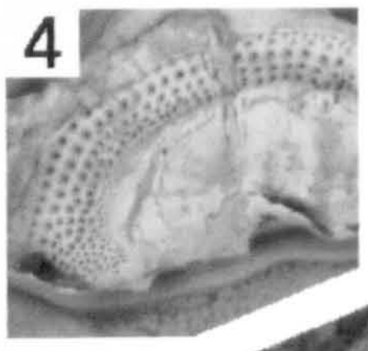
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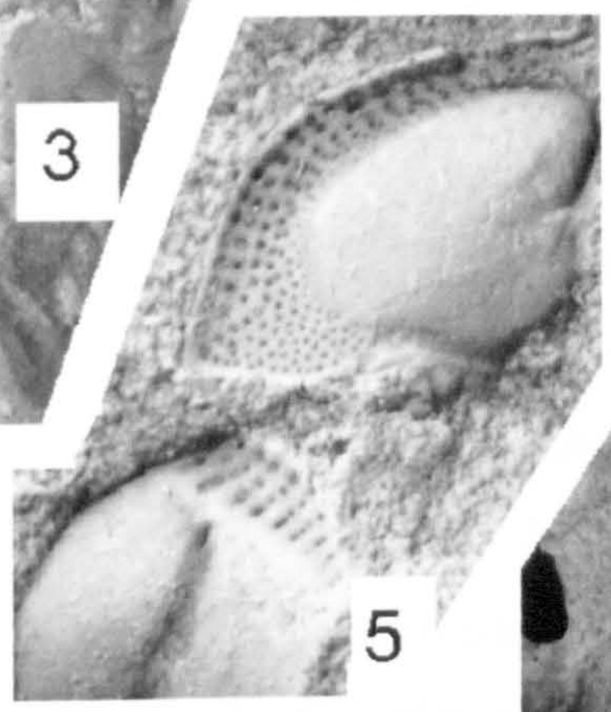
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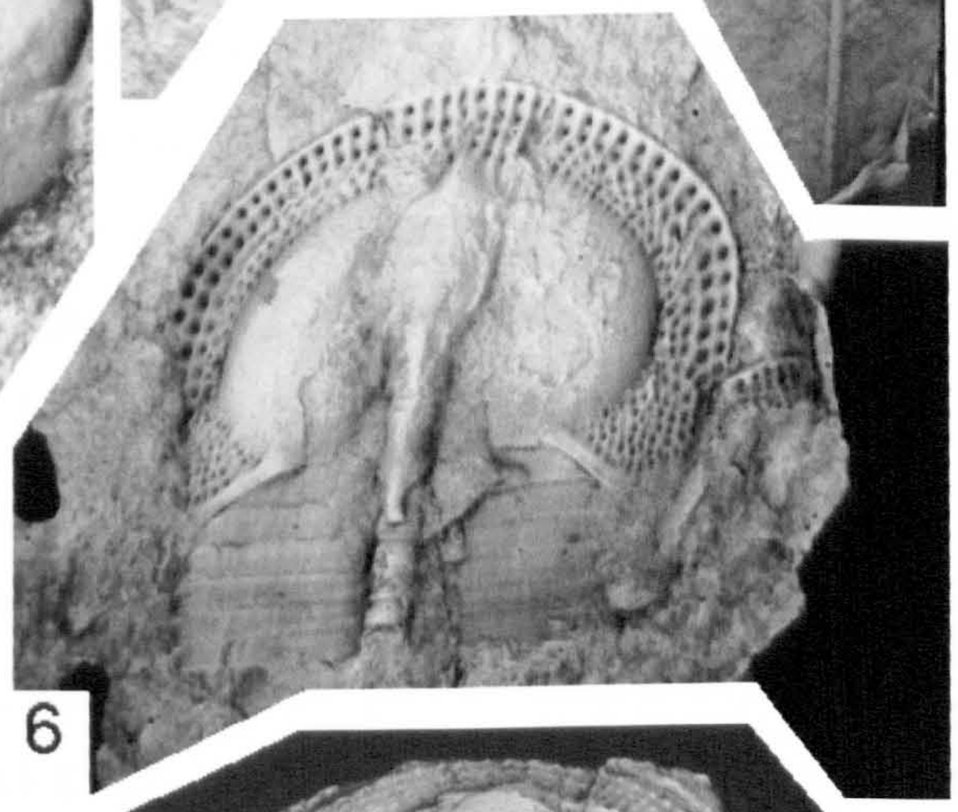
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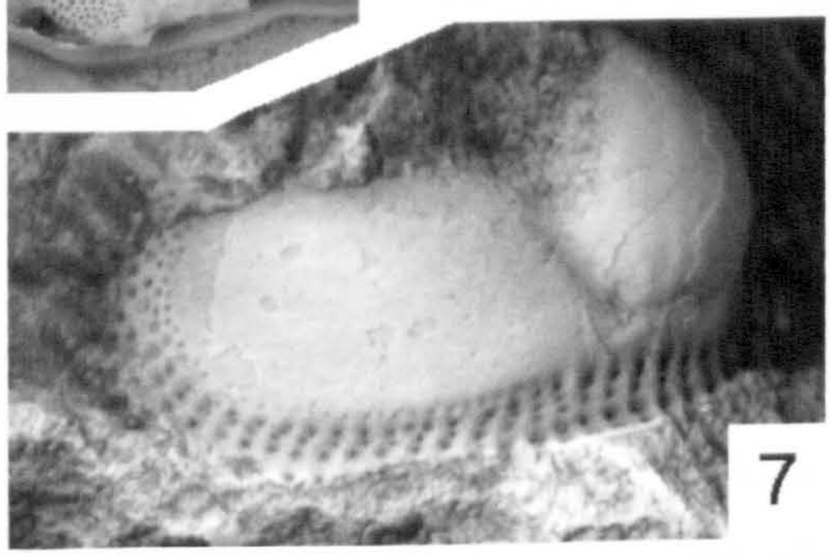
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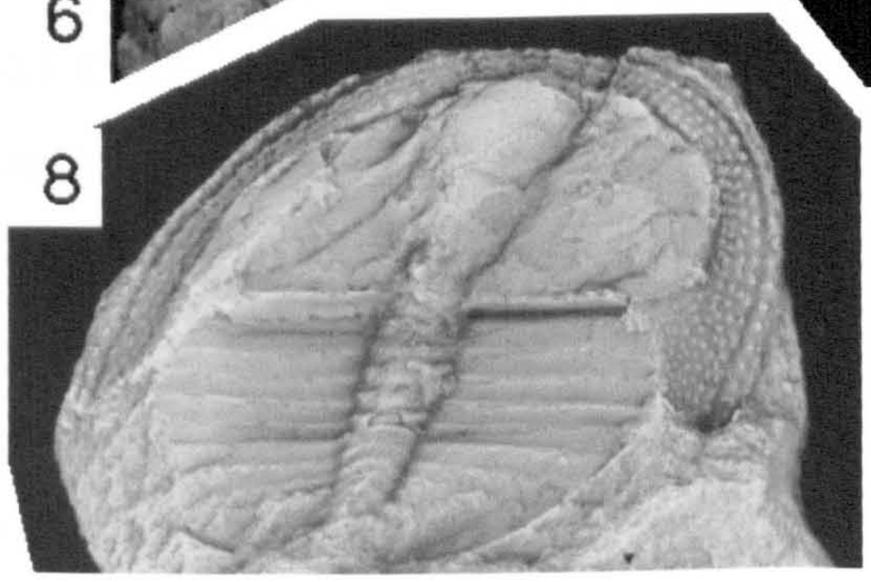
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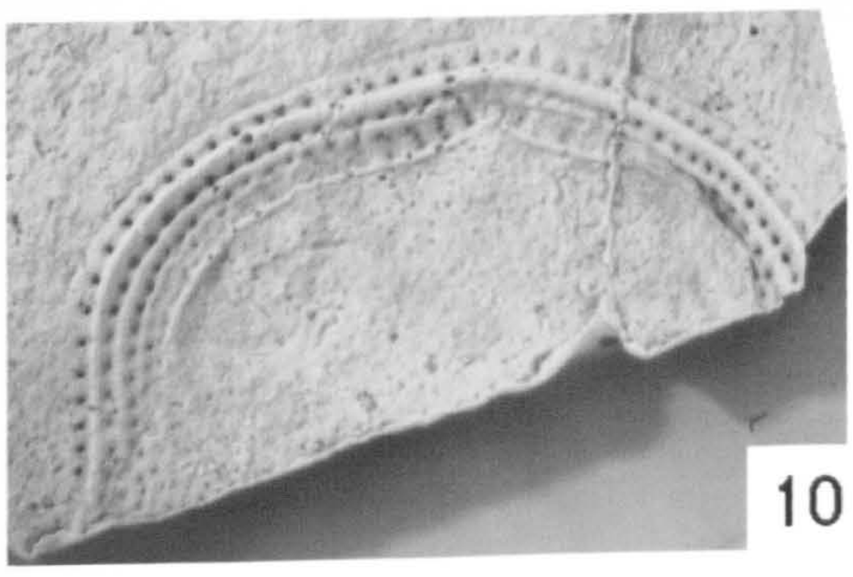
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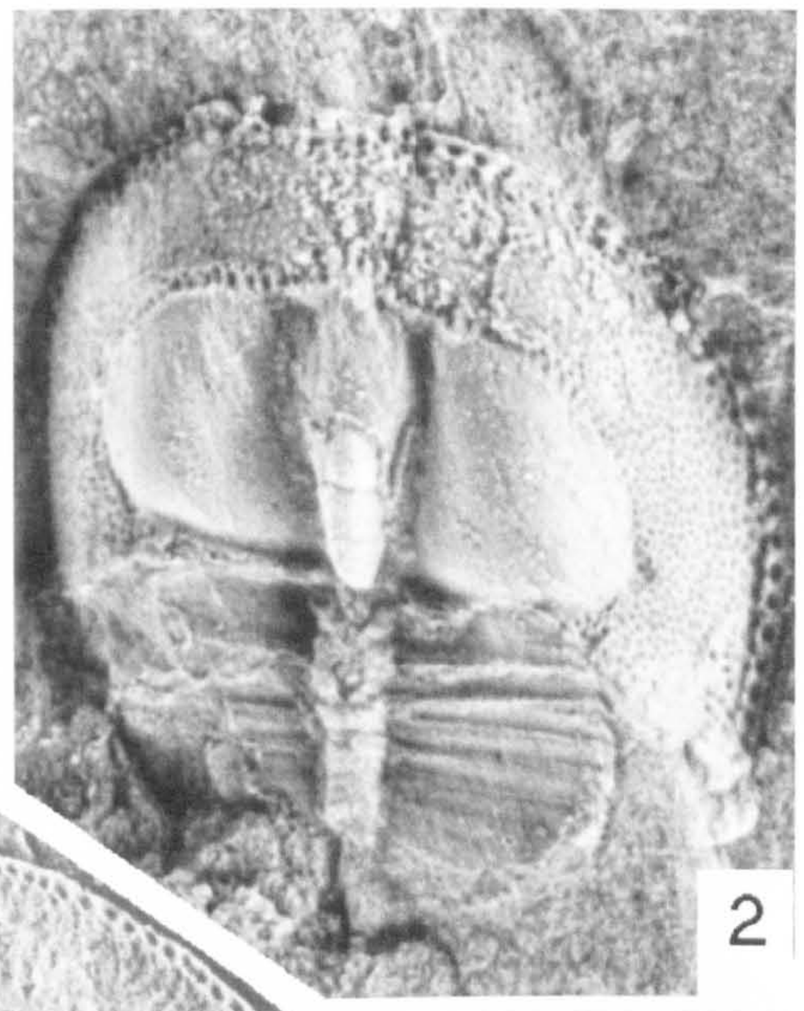
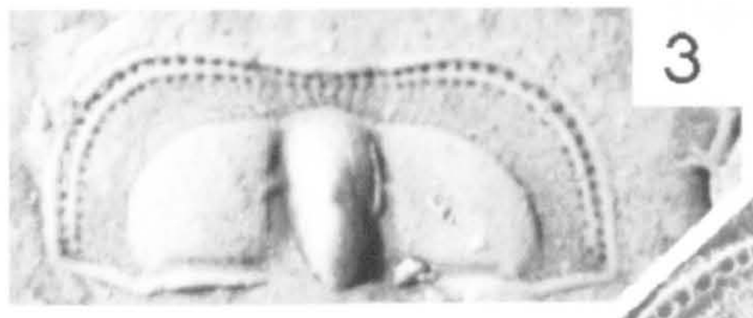
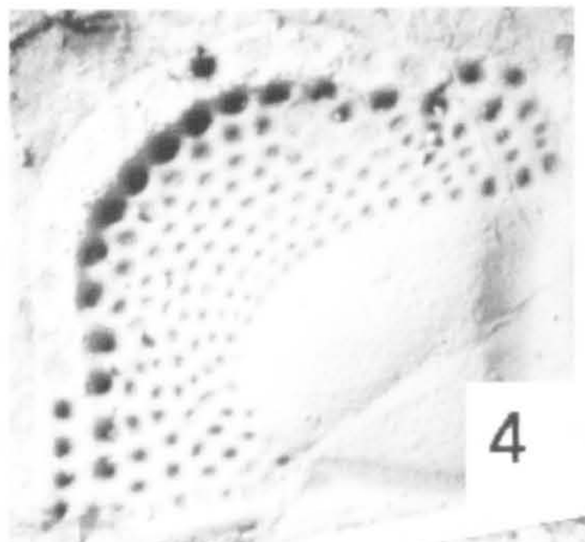
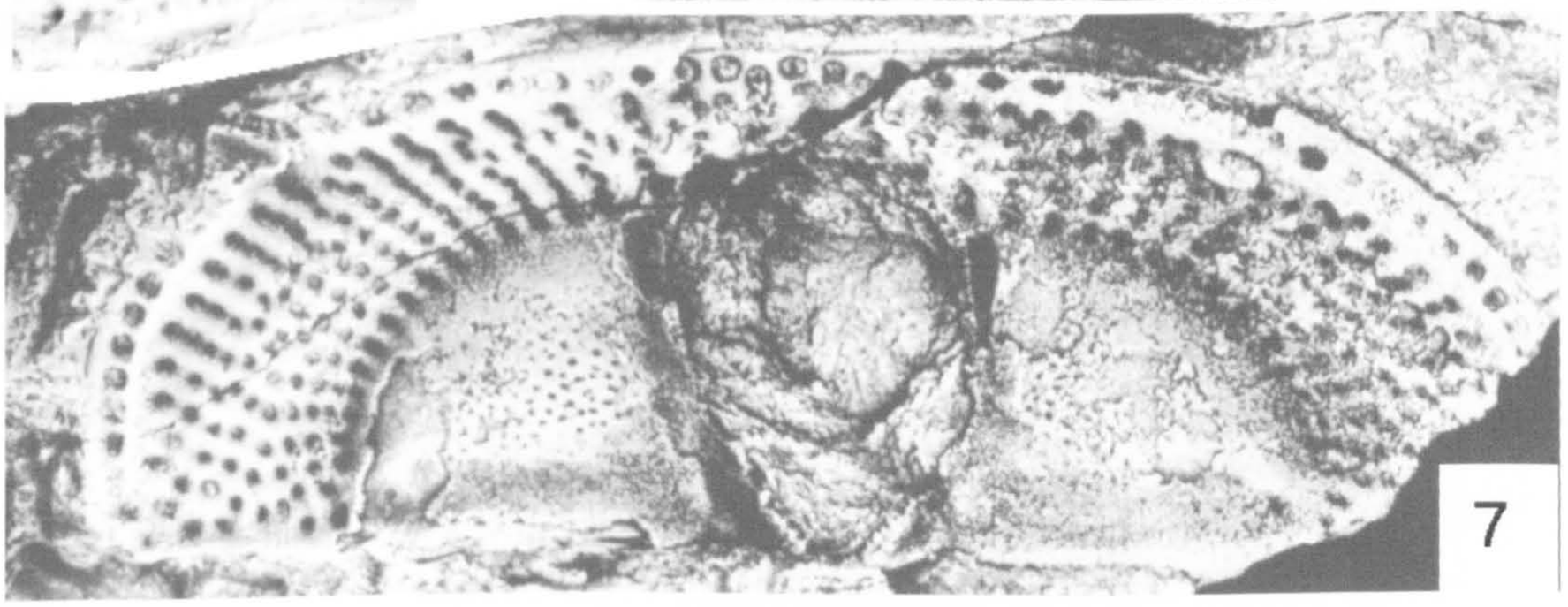
Explanation of Plate 9

1 and 2. *Protolloydolithus ramsayi* (Hicks, 1875). 1. BGS 410, latex peel from external mould, note worm casts under genal lobe. "*bifidus* Shales", Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone of stream section 305 m southwest of Pen-lan Farm, Lampeter Velfrey, Carmarthenshire, Wales, X3. 2, NMW 86.35G.276, ventral mould of near complete individual, previously figured by Kennedy (1989, pl. 8, fig. 11). Llanfallteg Formation, Lower Llanvirn Series, lower Abereiddian Stage, *artus* Biozone immediately behind Cefn-maen-llŵyd farmhouse at Rhyd-y-wrăch, Whitland, Wales, X5. 3. *Protolloydolithus neintianus neintianus* Whittard, 1956. BGS 92988, latex cast of external mould of cranidium of meraspid individual showing similar cephalic outline seen in *P. n. salax*, that becomes less pronounced in holaspid stage. Tuffs of the Stapeley Volcanic Member of the Hope Shale Formation, lower Llanvirn Series, lower Abereiddian Stage, upper *artus* Biozone of Tasgar quarries, 248 m NNW of entrance to Linley Drive, Shelve, Shropshire, England, X9. 4 and 6. *Protolloydolithus neintianus salax* (Rushton and Hughes, 1981), probably from the *artus* Biozone, lower Llanvirn Series of the Great Paxton Borehole, 8 km SW of Huntingdon, Cambridgeshire, England, 4. BGS 8529a, latex cast of external mould of partial cranidium, showing distinctive "kneeling mat" cephalic outline, X5. 6. BGS 8528, latex cast of partial cranidium, X4. 5. *Protolloydolithus* cf. *ramsayi*. PGS SG 6717, a single distorted internal mould of nearly complete upper lamella and external mould of part of lower lamella, figured by Romano(1990, text-fig. 3 [= *P.* sp.]). The Valongo Formation, Llanvirn, *Placoparia tournemini* Biozone of Covelo, Valongo, Portugal, X. 7. *Hanchungolithus*?. IGR 2635, latex cast of external mould of near complete cranidium, figured by Henry *et al.* (1993, fig. 2 [= *P.* sp.]), note the good radialy aligned pits, lack of I_n cut off, no F pits and a posterior fossula present. From the Andouillé Formation, Llanvirn Series, *Placoparia tournemini* Biozone, les Monneries, Andouillé, Armorican Massif, France, X8.









Explanation of Plate 10

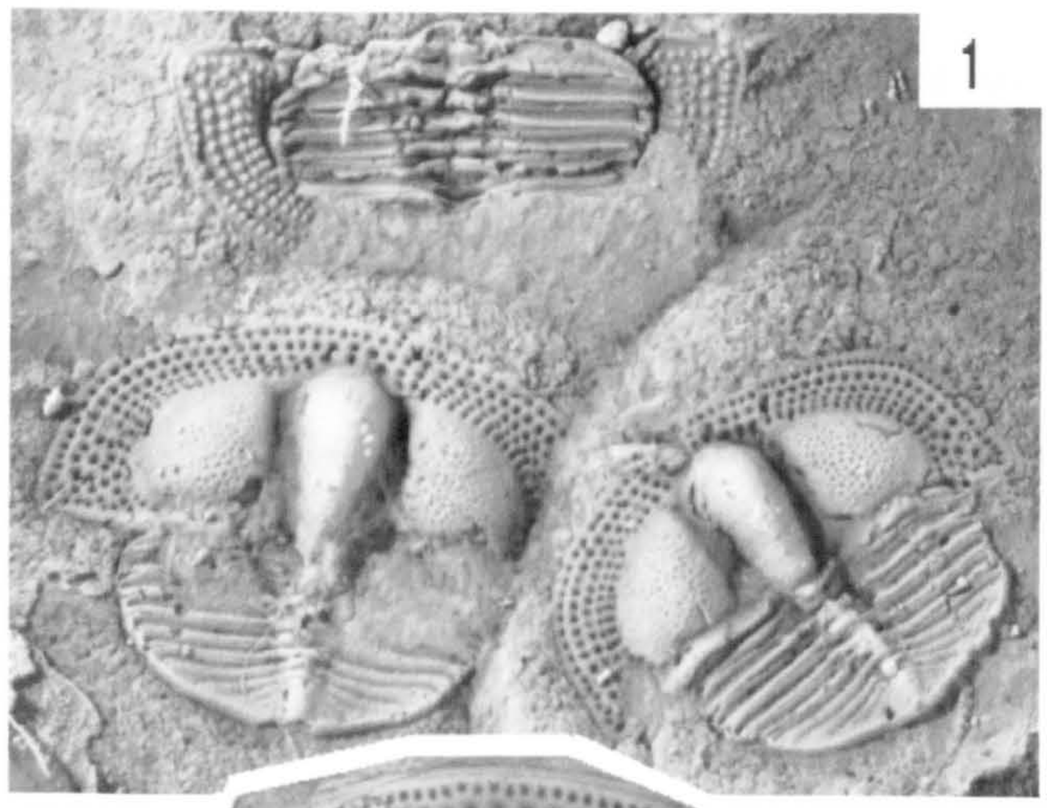
Figs 1-8. *Deanaspis goldfussii* (Barrande, 1846). 1., BNHM It1211, latex peel of two external moulds of cranidia and dorsal thacices and pydiia and one internal mould of enrolled individual all meraspid stage four, figured by Dean (1967, pl. 3, fig. 6, [as *Cryptolithus* ? *bedinanensis* sp. nov.]). From the Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, lower Cheneyan Stage of Dean locality B.6, SW of Bedinan, southern Turkey, X7. 2., UUG Xa324, testiferous cranidium, thorax and pygidum showing strong reticulation on glabella and genal lobes. From the Letná Formation, Beroun Series, (= low to middle Caradoc Series, Burrellian-mid Cheneyan stages, Letná, Bohemia, X4. 3., BNHM It 683, latex cast of external mould of partial cephalon showing slight invagination behind anterolateral angle of fringe, long genal spine, figured by Dean (1967, pl. 2, fig. 5, [as holotype of *Marrolithoides laticirrus* sp. nov.]). From the Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, upper Burrellian Stage of Dean locality B.3, SW of Bedinan, southern Turkey, X4. 4., BNHM It 718., latex cast of meraspid cranidium showing development of only two arcs. From the Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, upper Burrellian Stage of Dean locality B.8, SW of Bedinan, southern Turkey, X4. 5., BNHM It 708b, latex cast of cranidium and three thoracic segments, note lake of occipital spine and strong reticulate sculpture on glabella and genel lobes, figured by Dean (1967, pl. 2, fig. 13 [as paratype of *Marrolithoides laticirrus* sp. nov.]). From same horizon and locality as 3, X5. 6., BNHM It 734, latex cast of external mould of cranidium, figured by Dean (1967, pl. 2, fig. 8 [as holotype of *Cryptolithus? inferus* sp. nov.]). From the Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, upper Burrellian Stage of Dean locality B.1, SW of Bedinan, southern Turkey, X3.5. 7., BNHM It 852, latex cast of cranidium. From the Lower Shale Member of the Bedinan Formation, upper middle Caradoc Series, upper Burrellian Stage precise locality not recorded, SW of Bedinan, southern Turkey, X6. 8., MGS 1414, testiferous lower lamella showing braod girder and first internal pseudogirder. From Pres de l'oued Talrhent, Tafilalt district, Morocco, X5.

Figs 9-11. *Deanaspis primotina* sp. nov. all from siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua

Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series, Bou R'bia–Sidi Touhama, Coude du Dra, Anti Atlas Mountains, Morocco. 9. MGS 1604/4, holotype, internal mould of partial cranidium showing closely packed E_1 pits I_1 slightly larger than other pits but no increase in diameter posteriorly (as in *Onnia*), X7. 10., BNHM 1604/6, internal mould of nearly complete meraspid stage three individual, X10. 11., BNHM 1604/5, paratype, internal mould of ventral lower lamella showing equally developed girder and pseudogirder, X5.

Figs 12, 14. *Deanaspis pongerardi* (Rouault, 1847). 1., SMF 24823, internal mould of cranidium, figured by Hammann (1976, pl. 1, fig. 10 [as *Onnia* ? n. sp. aff. *grenieri*]). From the Upper "Bancs mixtes", possibly upper Caradoc-Ashgill, Sierra Morena, Spain, X4. 14., UUG JV 1103, internal mould of ventral lower lamella showing broad girder and first internal pseudogirder, note vincular notches on flange, figured by Shaw (1995, fig. 14-11 [as *Deanaspis vysocanensis* (Přibyl and Vaněk, 1969)]). From the Vinice Formation, Caradoc Series, upper Cheneyan Stage, Knížkovice, Bohemia, X3.75

Fig. 13. *Deanaspis linol* Šnajdr, 1981. MŠ 11156, partial internal mould of cranidium showing external mould of ventral surface of lower lamella, figured by Šnajdr(1981). From the Libeň Formation, Řevnice Quartzite, Rumpál Mountain near Rokycany, Bohemia.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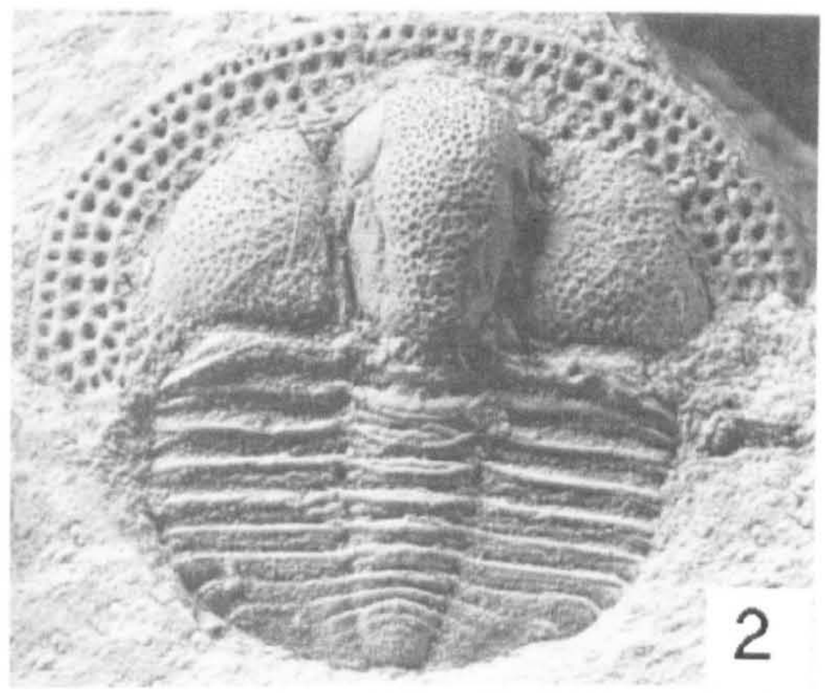
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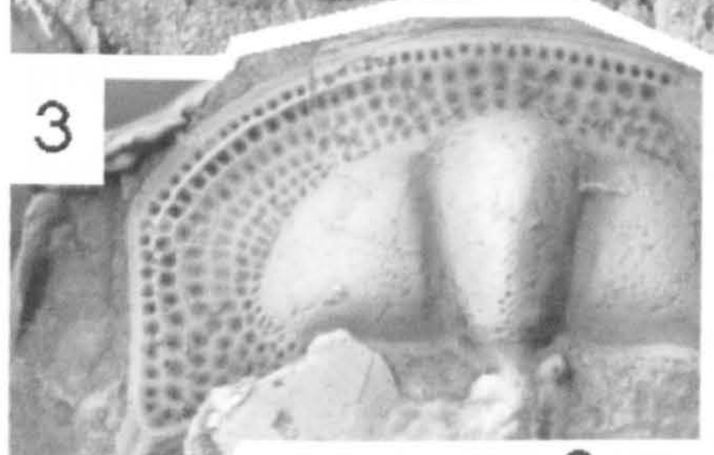
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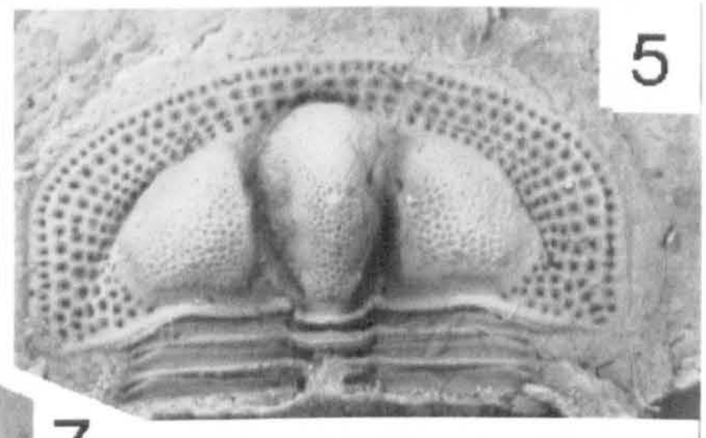
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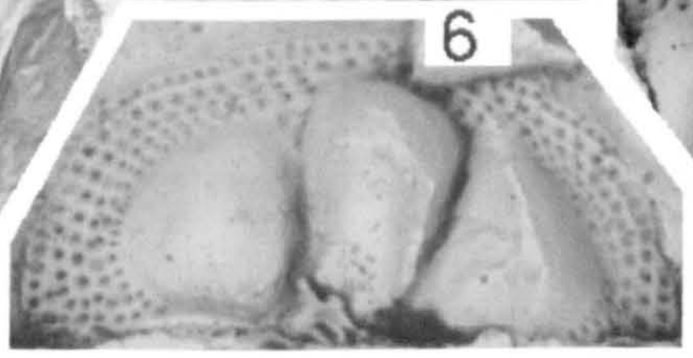
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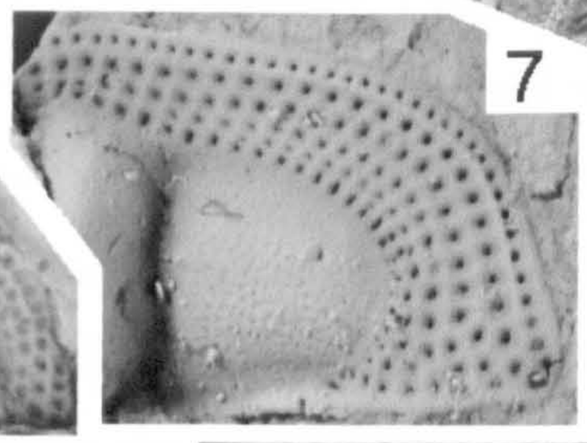
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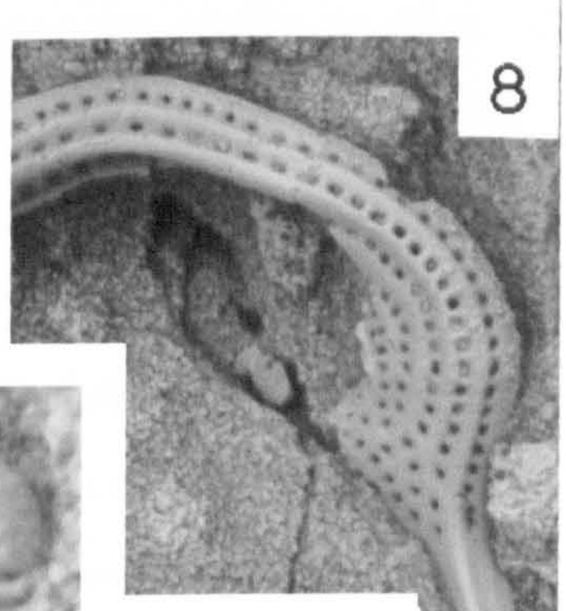
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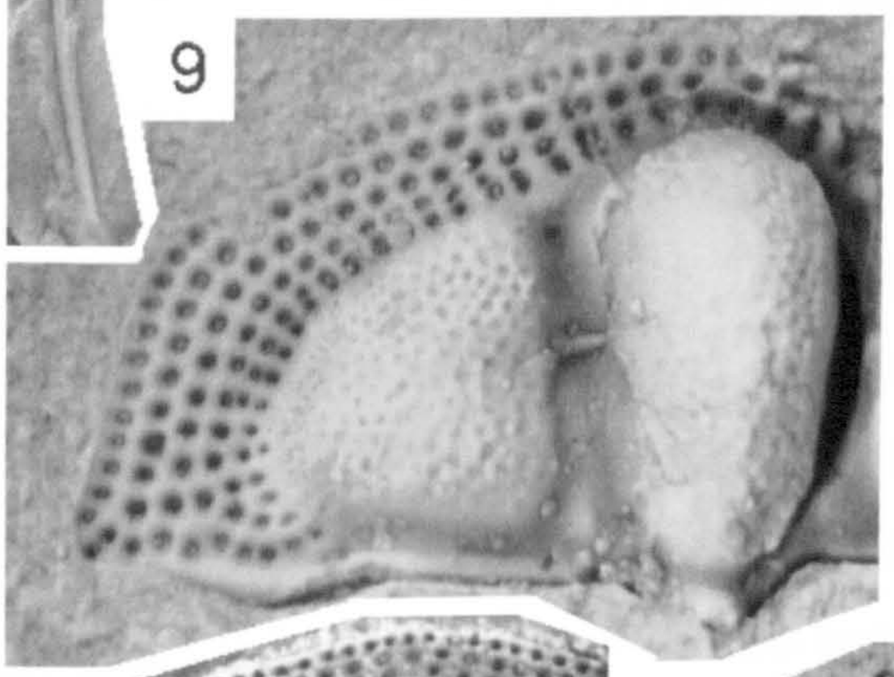
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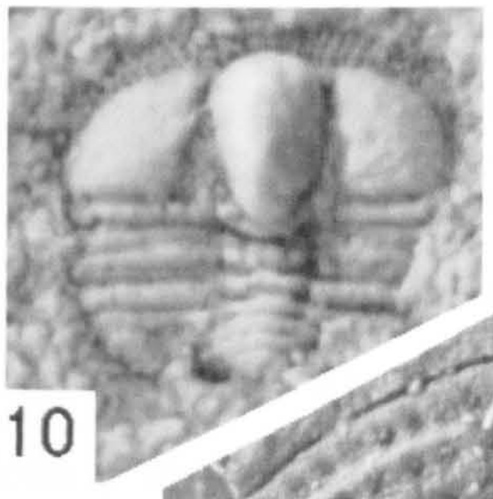
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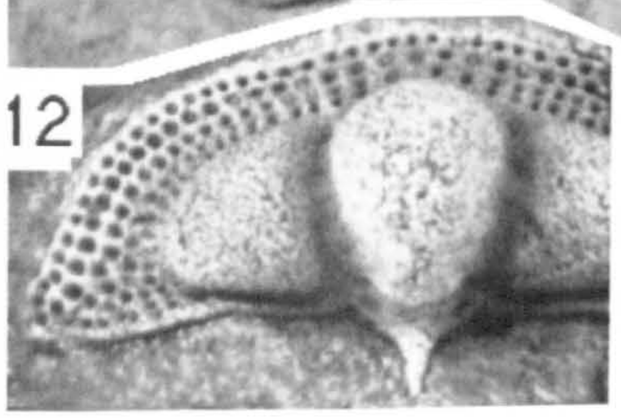
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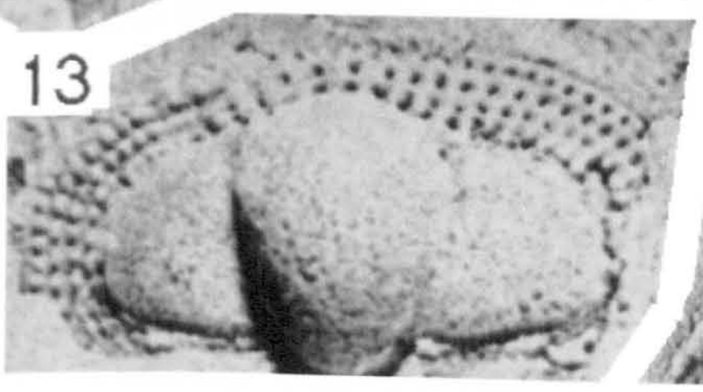
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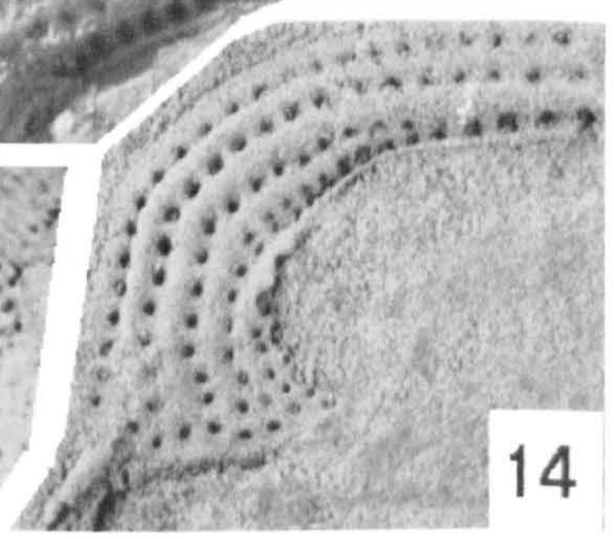
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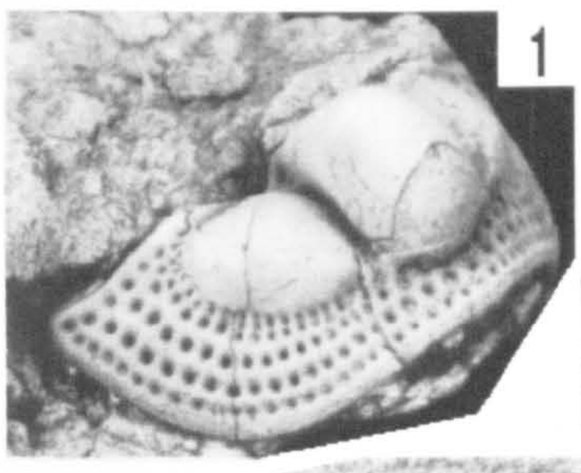
Explanation of Plate 11

Fig. 1., *Onnia ultima superba* (Bancroft, 1929). BNHM In 52011/1, testiferous cranidium showing larger I_1 pits than other arcs and a lack of I_2 pits frontally. From the upper Acton Scott Formation, Upper Caradoc Series, Onnian Stage, early *Onnia ultima superba* Local Range Zone, Onny River, south Shropshire, England, X3. 2., *Onnia ultima ultima* (Barrande, 1852). CNM L30817, partially testiferous nearly complete individual, note extensive pits in all arcs and lack of I_2 frontally figured by Shaw (1995, fig. 15-17). From the Králův Dvůr Formation, Ashgill Series, Královdvůr Stage of Kosov, Bohemia, X4. 3., *Onnia ultima canthyle* sp. nov. , MNM 11/2, testiferous damaged cranidium of probable late meraspid stage showing slight posterior inflation. From the upper-middle siltstones of the Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, upper Caradoc Series of Bou R'bia – Sidi Touhama, Coude Du Dra, Anti Atlas Mountains, Morocco, X6. 4., *Onnia ultima abducta* (Přibyl and Vaněk, 1969), CNM L30814, i nternal mould of nearly complete individual showing highly sigmoidal pygidium outline and variation in the packing of E_1 pits along the fringe, figured by Shaw (1995, fig. 15-8 [= *Onnia superba superba*]. From the Bohdalec Formation, upper Caradoc to lower Ashgill series, upper Beroun Stage of Malá Chuchle, Bohemia, X4. 5., *Onnia ultima canthyle* sp. nov. , MNM 11/1, holotype, testiferous cranidium showing slight posterior inflation, I_1 and I_2 pits increase in size posteriorly and no I_2 pits mesially. Same horizon and location as 3, X5. 6. *Onnia ultima canthyle* sp. nov. , MNM 831/1, partial internal mould of cephalon and external mould of ventral surface of lower lamella showing "spiculate" area around the genal lobe and distinct first internal pseudogirder channel. From Flanc Sud-Est of Jbel Lhadid, Oulmès, Central Hercynian Massif, Morocco, X5. 7. *Onnia ultima canthyle* sp. nov. , MNM 11/3, internal mould of pygidium showing smooth pleural lobes. Same horizon and location as 3, X6. 8. *Onnia ultima cobboldi* (Bancroft, 1929*b*). BGS PCT 4800, internal mould of cranidium. From Dufton Shale Formation, upper Caradoc Series, Onnian Stage, Pus Gill, Cross Fell Inlier, Northern England, X8. 9. *Onnia ultima creta* Owen & Ingham, 1988. GLA HM A15073/1 testiferous cranidium, paratype, showing distinct internal lists and reticulate glabella. From upper Acton Scott Formation, upper Caradoc Series, Onnian Stage, *O. s. creta* Local Range Zone, Onny River section, south Shropshire, England, X5. 10-12. *Onnia ultima cobboldi* (Bancroft, 1929*b*), all from sandstones of the Upper Ktaoua

Formation, Ktaoua Clay and Sandstone Group, the lowest Ashgill Series, Jbel bou Debgane, Bou Haiara, Zegdou, Anti Atlas Mountains, Morocco. 10., MNM 901/1 damaged testiferous cephalon, X5. 11., MNM 901/2 damaged testiferous cephalon, X5. 12., MNM 901/3 testiferous lower lamella showing large I_1 pits, indistinct girder and distinct first internal pseudogirder, X5.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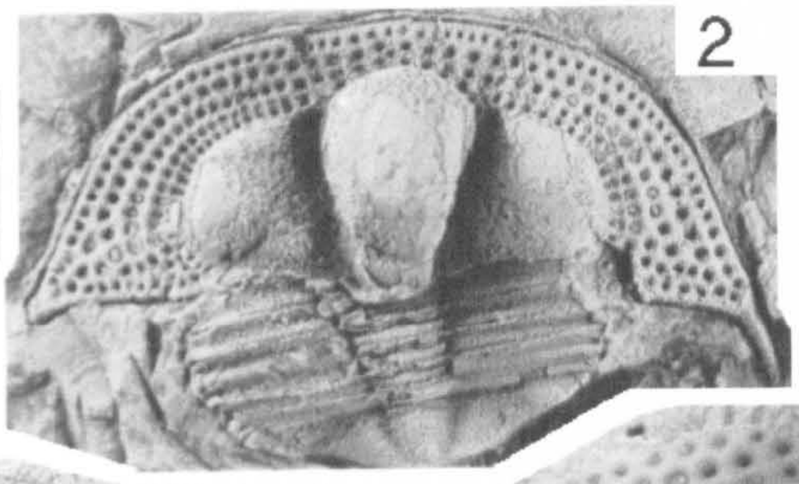
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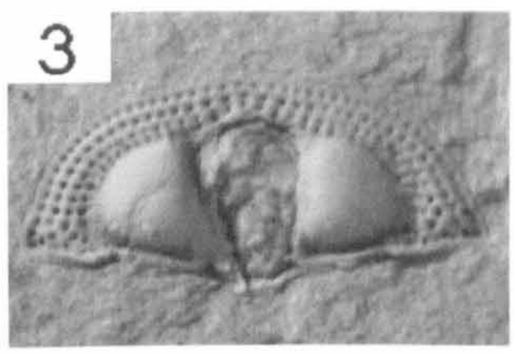
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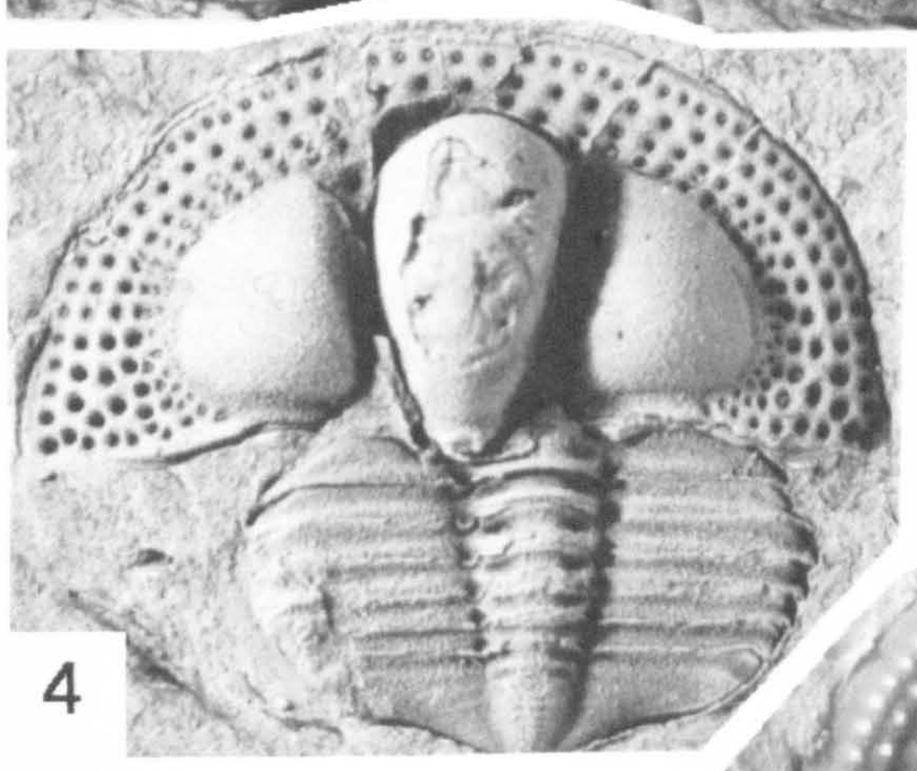
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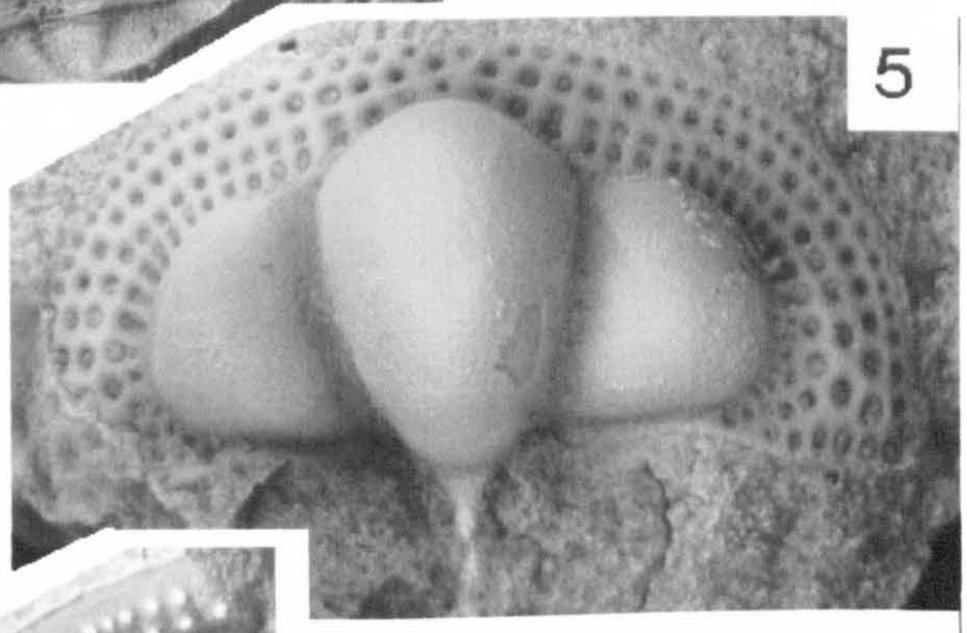
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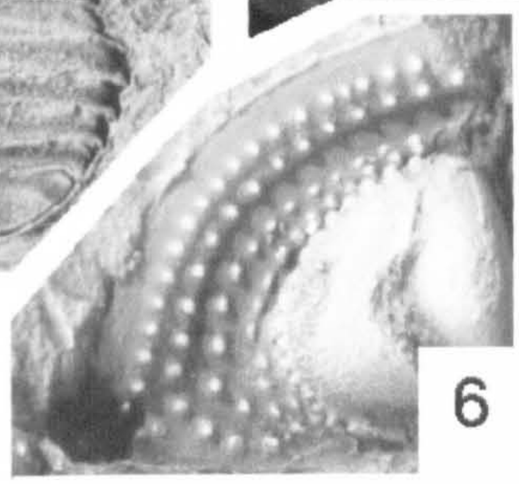
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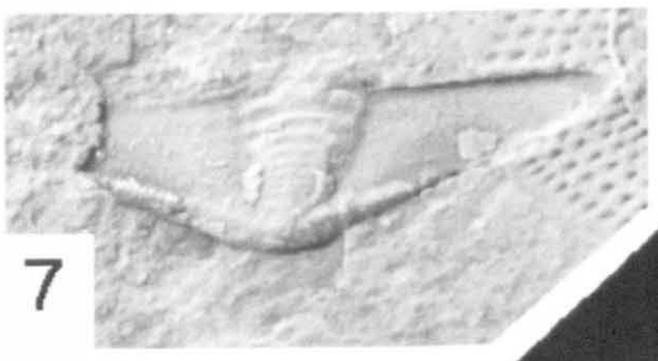
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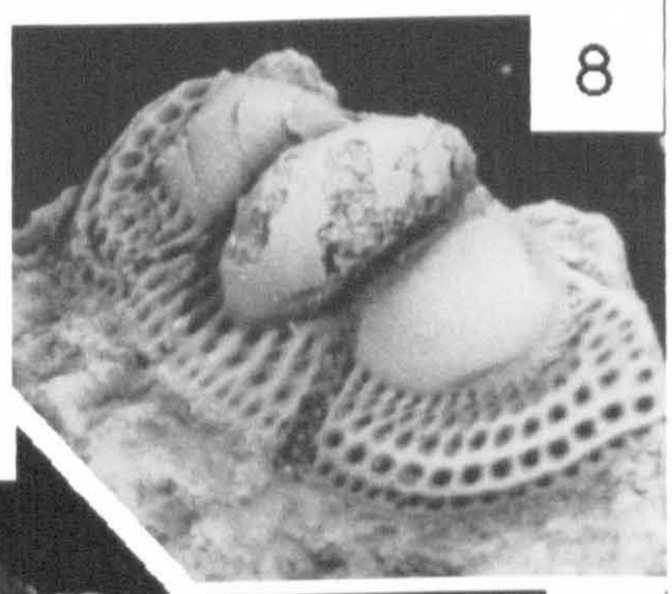
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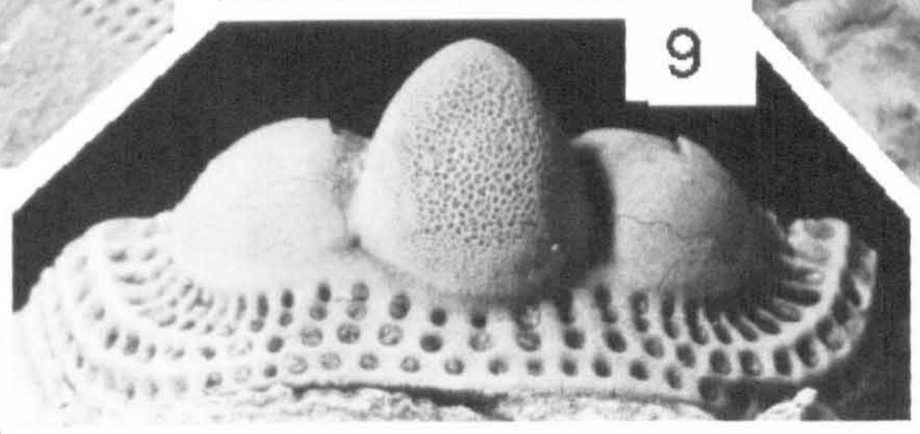
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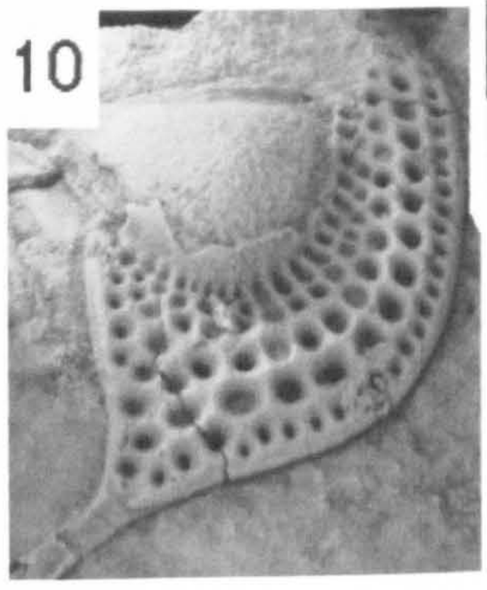
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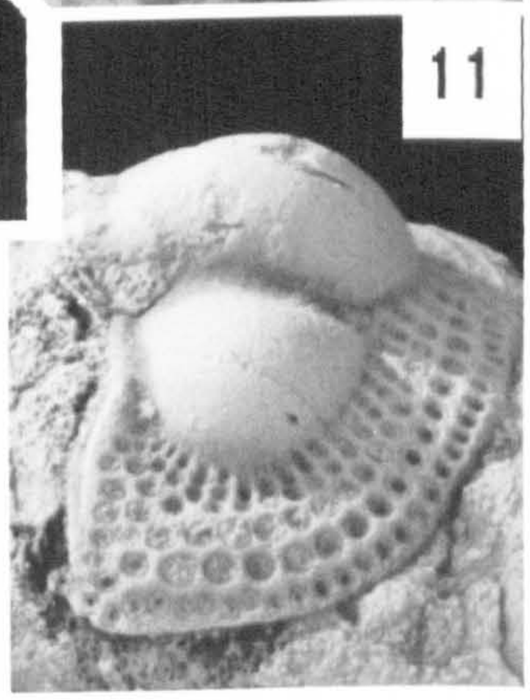
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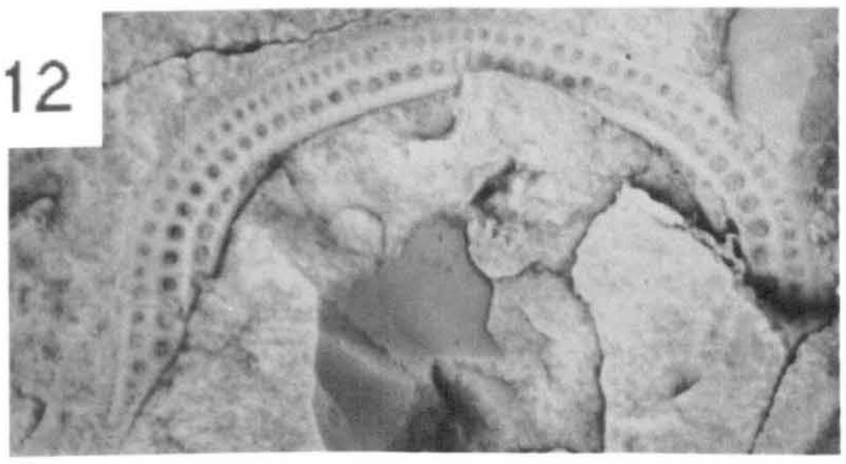
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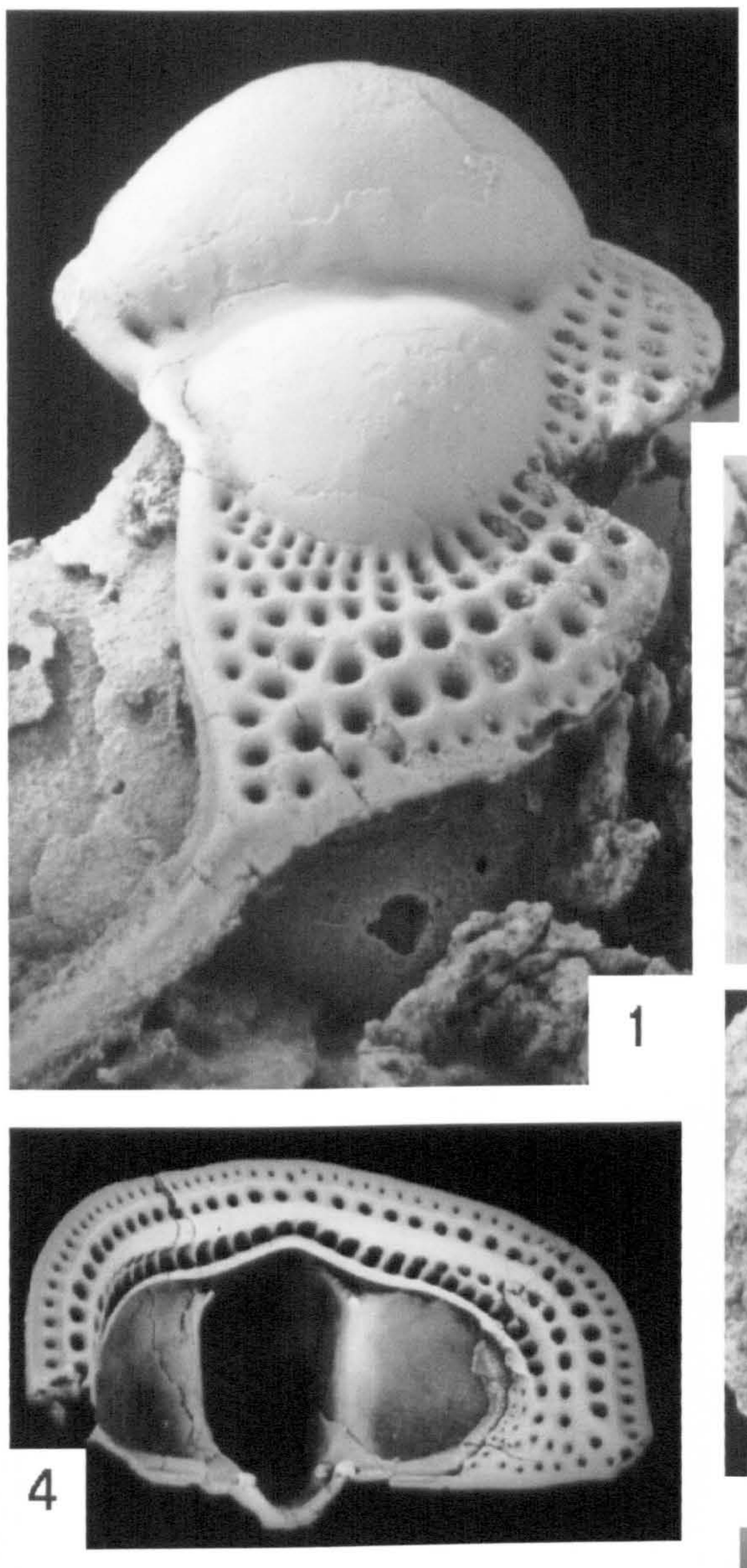
Explanation of Plate 12

Figs 1-5. *Onnia gracilis* (Bancroft 1929). 1, 2, 4., all from Upper Ktaoua Formation, upper Ktaoua Clay and Sandstone Group, lower Ashgill Series, Jbel bou Dedgane, Bou Haiara, Zegdou district, Anti Atlas Mountains, Morocco. 1., MGS 1651/2, damaged testiferous cephalon showing distinct I_2 mesially, large I_1 and I_2 arcs that are slightly raised posteriorly note typical "star" arrangement of pits posteriorly as seen in many specimens of *O. gracilis* (see also Fig. 3), X10. 2, 4., MGS 1651/1 silicified cephalon showing I_2 arc mesially, I_n cut off by I_3 and F pits and vincular notches on lower lamella flange, X6. 3., BNHM In52017/3, damaged testiferous cranidium showing I_2 arc mesially, large I_1 and I_2 pits posteriorly "star" arrangement of pits posteriorly and lacking I_4 arc. From from the upper part of the Wistanstow Member of the Acton Scott Formation, middle Onnian, upper *clingani* Biozone, Onny River, south Shropshire, England. 5., MGS 1778, damaged testiferous cranidium showing I_2 arc sulcate with In mesially. From the Ouaouglout Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lowest Caradoc Series (= Aurelucian Stage), Alkhikh-Tazzarine, Tarbolt distrct, Anti Atlas Mountains, Morocco, X8.

Figs 6-8. *Onnia etyma* sp. nov., all from siltstones equivalent stratigraphically to the Lower Tiouririne Sandstone Member, Lower Ktaoua Formation, Ktaoua Clay and Sandstone Group, lower Caradoc Series, Bou R'bia–Sidi Touhama, Coude du Dra, Anti Atlas Mountains, Morocco. 6., MGS 1604/1, holotype, internal mould of partial cranidium showing all pits of similar diameter, I_n cut off by I_4, F pits extend forward between I_n and genal lobe and faint reticulate sculpture on genal lobe, X5. 7., MGS 1604/2, paratype, latex cast of ventral mould of lower lamella showing all pits of similar diameter, lack of I_2 pits mesially, weak girder, distinct first internal pseudogirder frontally, I_n cut off by I_4 arc and flange pits, X6. 8., MGS 1604/3, paratype, latex cast of internal mould of pygidium showing distinct axial rings and interpleural furrows and steep posterior border, X5.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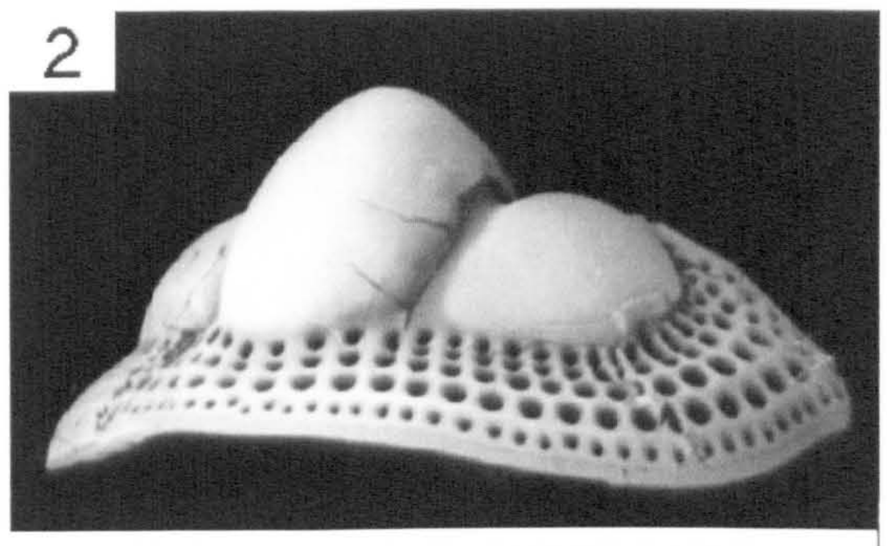
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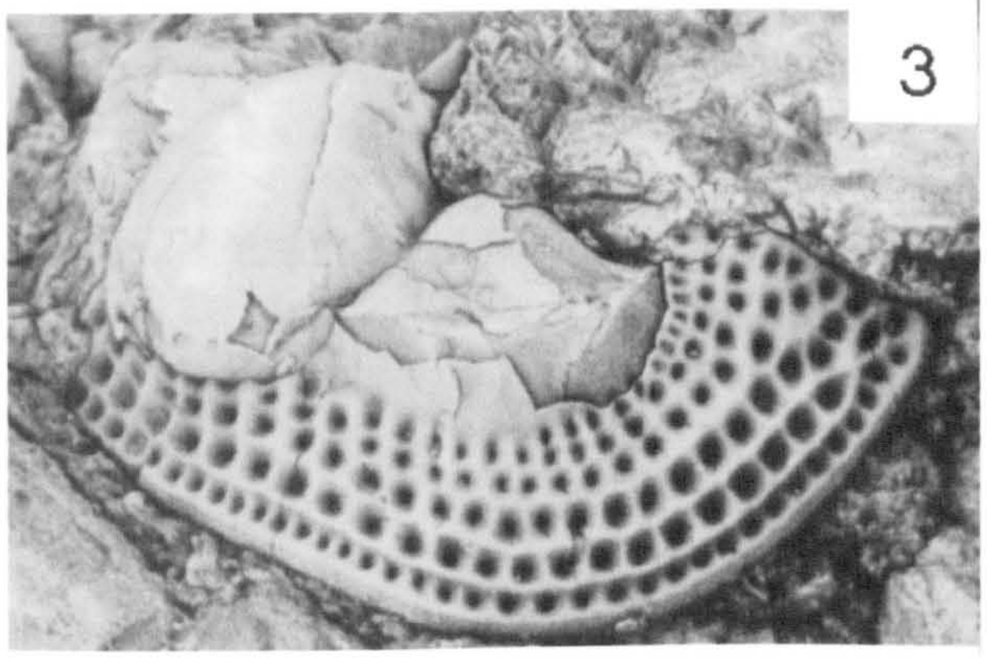
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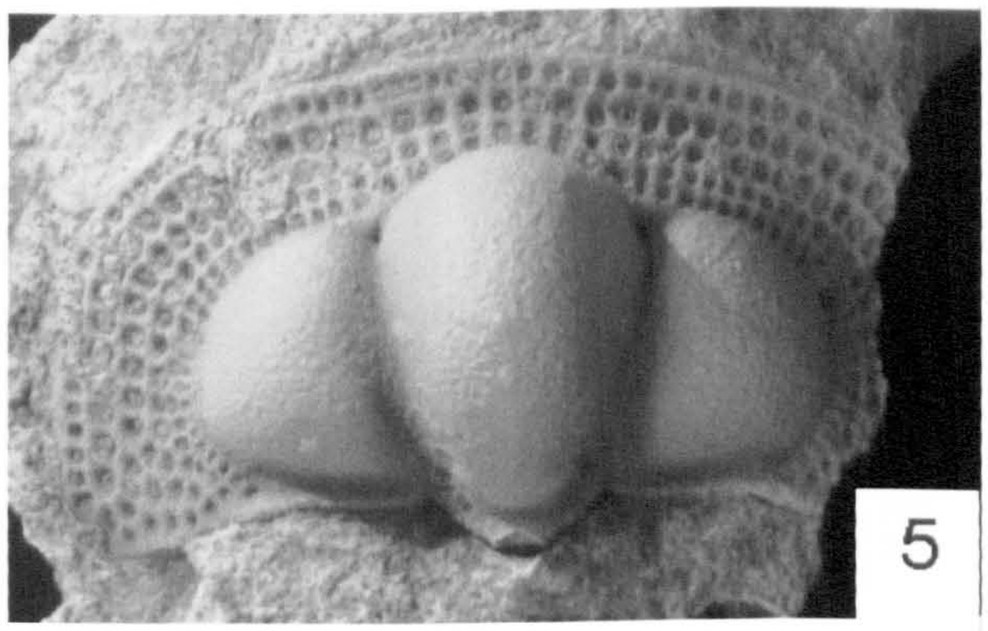
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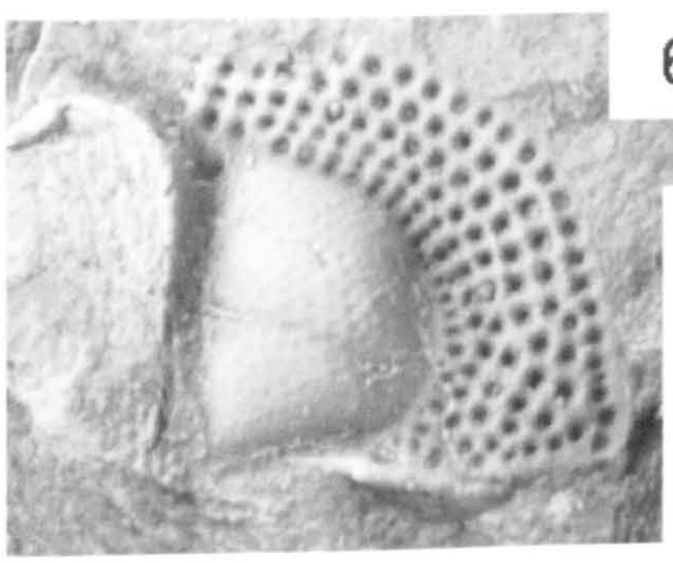
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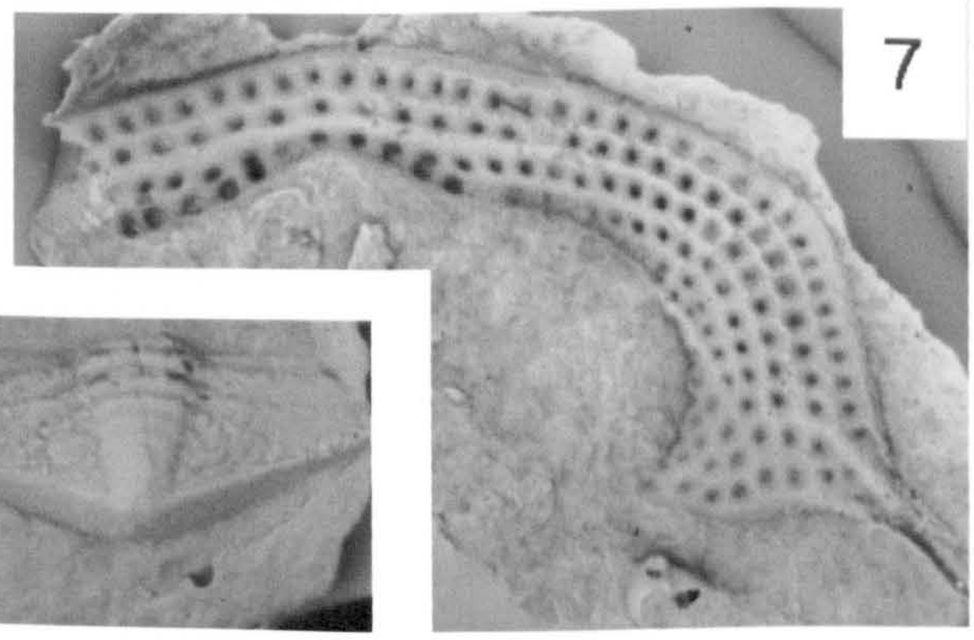
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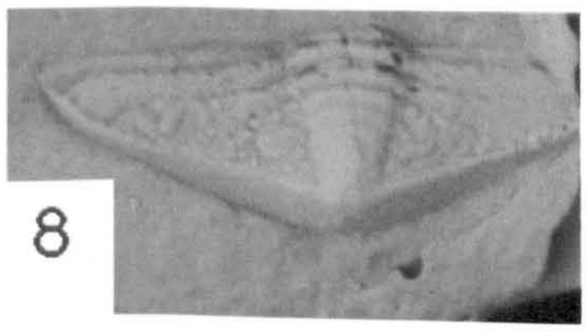
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5 Ordovician Palaeogeography and Stratigraphy

5.1 The Ordovician World

Text-Fig 5.1. Representation of the Ordovician showing the main area of Gondwana during the Arenig (from Cocks, 2001).

Gondwana was the largest continent during the Ordovician. It stretched from the South Pole to a latitude of over 30°N (see Text-fig. 5.1, Tobin & Walker 1997 and Cocks 2000). Indeed, palaeomaps are often difficult to compare as authors, naturally, centre their reconstructions on their particular area of interest. As a great deal of work is based along the Iapetus Ocean margin, the major area of Gondwana's landmass is rarely seen.

At the beginning of the Ordovician, Gondwana comprised Avalonia (England, Wales, SE. Ireland and parts of easternmost North America), Armorica (northern France), Perunica (Bohemia), Africa, South America, the Iberian peninsula, Italy, the Middle East, India, Australia, New Zealand, Antarctica and portions of China and Indonesia (see Text-Fig. 5.1a). Only Laurentia (most of North America and Greenland), Siberia and Baltica were separate from Gondwana. The Iapetus Ocean and its eastern extension, the Tornquist sea, separated Laurentia, Baltica and part of Gondwana. The vast ocean surrounding Gondwana to the east of Siberia and Baltica (which covered half the globe) has been referred to (variously) as the Pacific Ocean, the Mozambique Ocean (Dalziel 1997) and the Panthalassic Ocean (Cocks and Torsvik 2002).

Palaeomagnetic data have given relatively precise latitude locations of most plates. During the Ordovician the South Pole was over northern Africa, pin-pointing precisely that part of Gondwana. However, Colombia, the north-western margin of the neighbouring South America, is depicted to be anywhere from 30°S (Torsvik 1998, van Staal *et al.* 1998) to 55°S (Cocks 2000) during the Arenig, a considerable distance. The palaeolatitude of Laurentia remained equatorial throughout the Ordovician (also shown by facies and faunal data (Cocks and Fortey 1982). Hoffman (1996) and van Staal *et al.* (1998) suggested that the Amazonia plate was separate from Gondwana during the Neoproterozoic and was part of a separate landmass comprising Laurentia, Baltica and Siberia, with rifting of the individual continents around 600-500Ma. Astini *et al.* (1995) suggested that the problematical Precordillera of northwest Argentina, a Laurentian derived terrane, rifted off in the Cambrian and drifted to the high latitude Gondwanan margin. Dalziel (1997) also suggests locations for the Neoproterozoic super continents Rodinia and later Pannotia in which Gondwana, Laurentia, Baltica and Siberia were all connected.

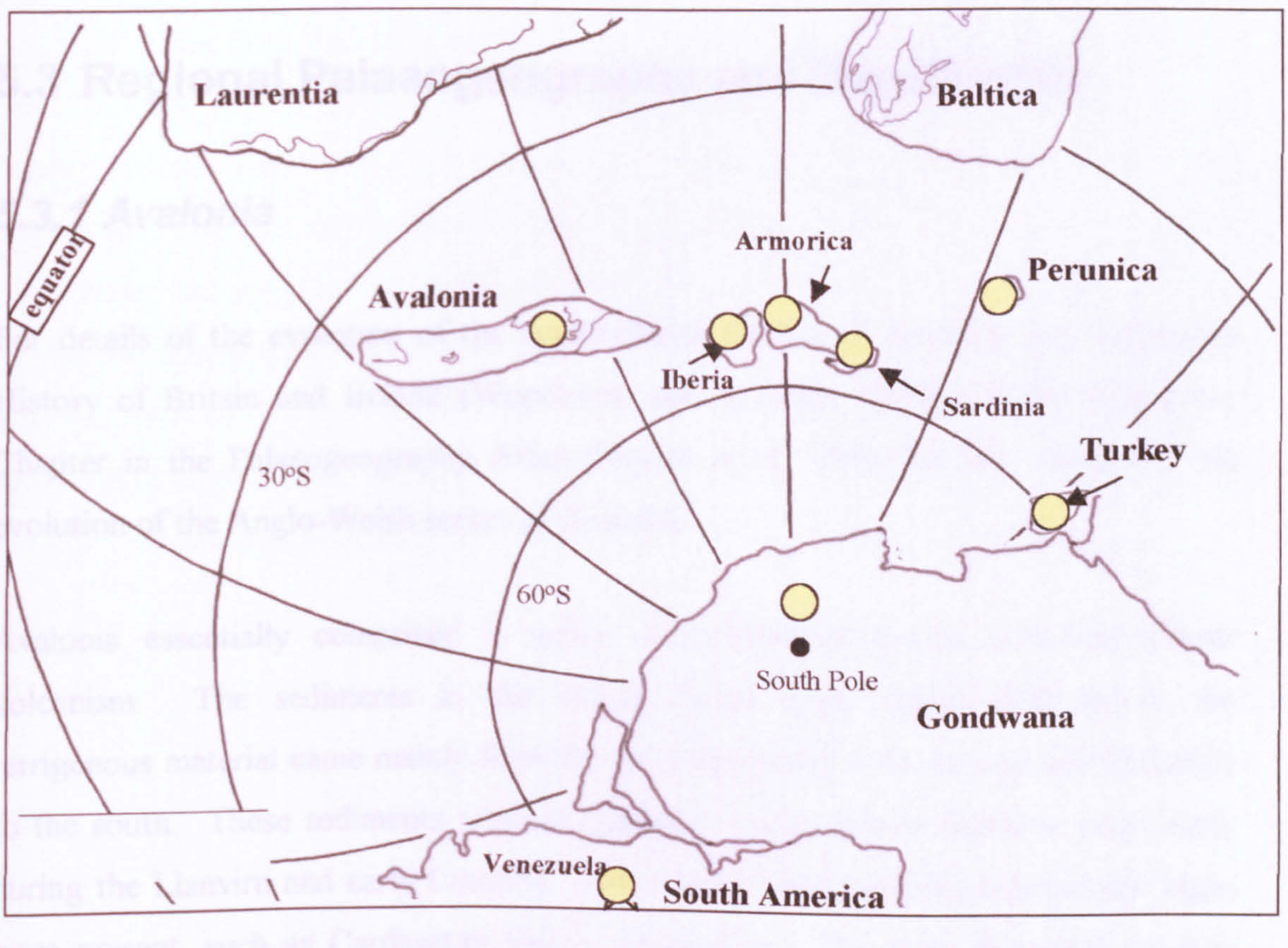
Avalonia is commonly viewed as two sections; the western half contains fragments now found in the Appalachians and Newfoundland, and the eastern section comprising England, Wales southeastern Ireland and northern Belgium. The precise location of Avalonia before rifting from Gondwana and the time that rifting occurred has long been debated. Some workers show Avalonia next to the north-western African margin of Gondwana (Rast and Skeehan 1983, Torsvik 1998) others, based mainly on geochemical and tectonic data, show it as having an Amazonian cratonic basement and argue that it spanned the South American and north westernmost African margins (Nance and Murphy 1994, Dalziel 1997, van Staal *et al.* 1998; Murphy *et al.* 1998, Alvaro *et al.* 1999, Cocks 2000). McNamara *et al.* (2001) used new palaeomagnetic data from upper Neoproterozoic rocks in the southern Burin peninsula in Newfoundland to show a palaeolatitude of 34°S, which would coincide with that of the West African margin.

It is widely accepted that Avalonia rifted from Gondwana in the Arenig, opening up the Rheic Ocean (Cocks and Fortey 1982, van Staal *et al.* 1998, Torsvik 1998, Cocks 2000). However, Dalziel (1997) showed a distinct separation between Avalonia and Gondwana by Mid-Cambrian times, with the eastern half of Avalonia moving northwards at a greater rate than the western half producing an anticlockwise rotation, and remaining very close to Baltica as it moved northwards. A similar motion for Avalonia was proposed by van Staal *et al.* (1998) but with a slightly greater distance between Avalonia and Baltica. This scenario would then allow western Avalonia's eventual sinistral accretion onto Laurentia (Keppie 1993; Murphy *et al.* 1999).

The positions of Armorica, Iberia, Perunica and Turkey are not shown in many published reconstructions but when they are included they are always along the Iapetan margin of Gondwana. Alvaro *et al.* (1999) used the biogeographical distribution of Middle Cambrian trilobite taxa to place the terranes in an arc along the Gondwanan margin, see Text-fig. 5.2. Van Staal *et al.* (1998) showed Armorica rifting from the Moroccan margin of Gondwana by the early Arenig, and Torsvik *et al.* (1996) had the Bohemian Massif (Perunica) rifting off Armorica, which was connected to Morocco, during late the Llanvirn (Llandeilian). Tait *et al.* (1995), using palaeomagnetic data, estimated that Bohemia had rifted from Gondwana by Caradoc-Ashgill times.

The Ordovician was part of a very long period of greenhouse climate conditions, punctuated by a short-lived glacial event in the late Ashgill (e.g. see Brenchley *et al.* 1994). However, glacial sediments dating from the lowest Caradoc through the glacial height in the Ashgill and into the Silurian have been recognised from the northern margin of Gondwana, i.e., South America (Astini 1999), Morocco (Destombes, 1968b), Turkey (Dean 1992). This part of Gondwana was situated close to the south pole for some considerable time with the Saharan region as the glacial centre. Hamoumi (1999) has documented the rise of glaciation and the fluctuations through the Caradoc and into the Ashgill.

5.2 Distribution of the Marrolithinae



Text-Fig. 5.2. Map showing the locations of the marrolithine genera during the Ordovician (based on Cocks 2000).

During middle Ordovician times the Marrolithinae were widespread along the margins of Gondwana in Turkey, Morocco, and Venezuela. They are also associated with the micro-continents that rifted off the supercontinent: Avalonia, Armorica, Iberia, Sardinia and Perunica, such that now they are found in the Anglo-Welsh area, Armorica, the Iberian peninsula, Sardinia and Bohemia (see Text-fig. 5.2). Within each region, species were subjected to fluctuations in a range of environmental parameters such as sea temperatures, sediment input, volcanism (especially in the Welsh Basin) and glacial proximity. Turkey and Morocco were very close to the land-based glacier at that time centred on the Saharan Region of North Africa.

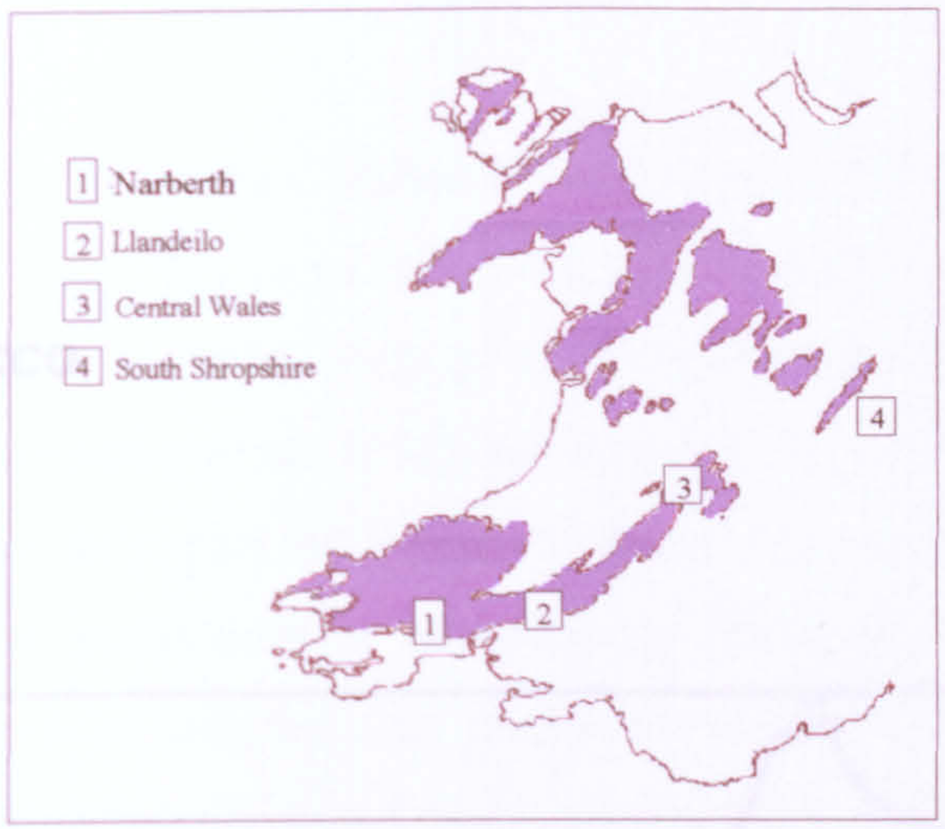
Using the evolutionary and migration patterns of the Marrolithinae the locations of the terranes involved and their distribution along the Iapetan margin will be clarified.

5.3 Regional Palaeogeography and Stratigraphy

5.3.1 Avalonia

For details of the evolution of the Anglo-Welsh section of Avalonia see Geological History of Britain and Ireland (Woodcock and Strachan 2000) and the Ordovician Chapter in the Palaeogeography Atlas (Bevins *et al.* 1992) for the details of the evolution of the Anglo-Welsh sector of Avalonia

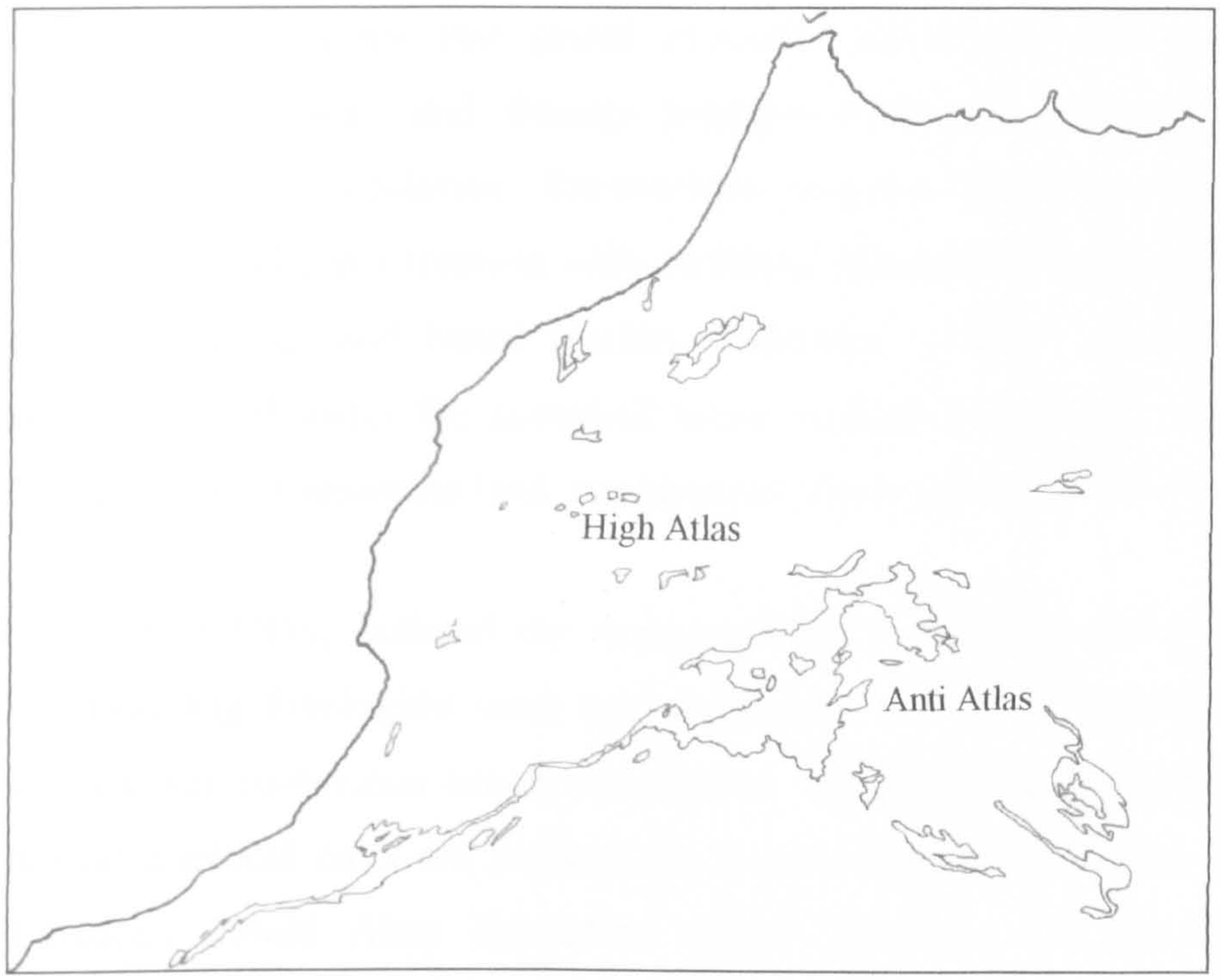
Avalonia essentially comprised a series of extensional basins with intermittent volcanism. The sediments in the Welsh Basin were typical shelf facies, the terrigenous material came mainly from the Midland platform to the east and Pretannia to the south. These sediments were interspersed with volcanic deposits, particularly during the Llanvirn and early Caradoc. Some local, fault-bounded topographic highs were present, such as Cardington Hill in Shropshire. The basin deepened towards Central Wales with shallow shelf deposits along the arc from St. David's on the Pembrokeshire coast through Narberth, Llandeilo to Shropshire (see Text-Fig. 5.3).



Text-Fig. 5.3. Map of Ordovician outcrops in England and Wales. Generally the shallow shelf deposits are found along the arc from Narberth to Shropshire, and deeper deposits toward Anglesey.

Avalonia rifted from the Gondwanan margin during the early Ordovician (Prigmore *et al.* 1997) and moved northwards towards Laurentia and Baltica, widening the Rheic Ocean which separated it from Gondwana. The most up to date summary of the stratigraphy of the Ordovician of the Anglo-Welsh sector of Avalonia and its correlation was provided by Fortey *et al.* (2000). This included some major changes to the chronostratigraphical framework adopted for the Anglo-Welsh Ordovician (see also Fortey *et al.* 1995) and significant revision to the lithostratigraphy of many of the local successions made since the correlation charts published by Williams *et al.* (1972). The latter publication remains an important "way-in" to the earlier literature.

5.3.2 Morocco



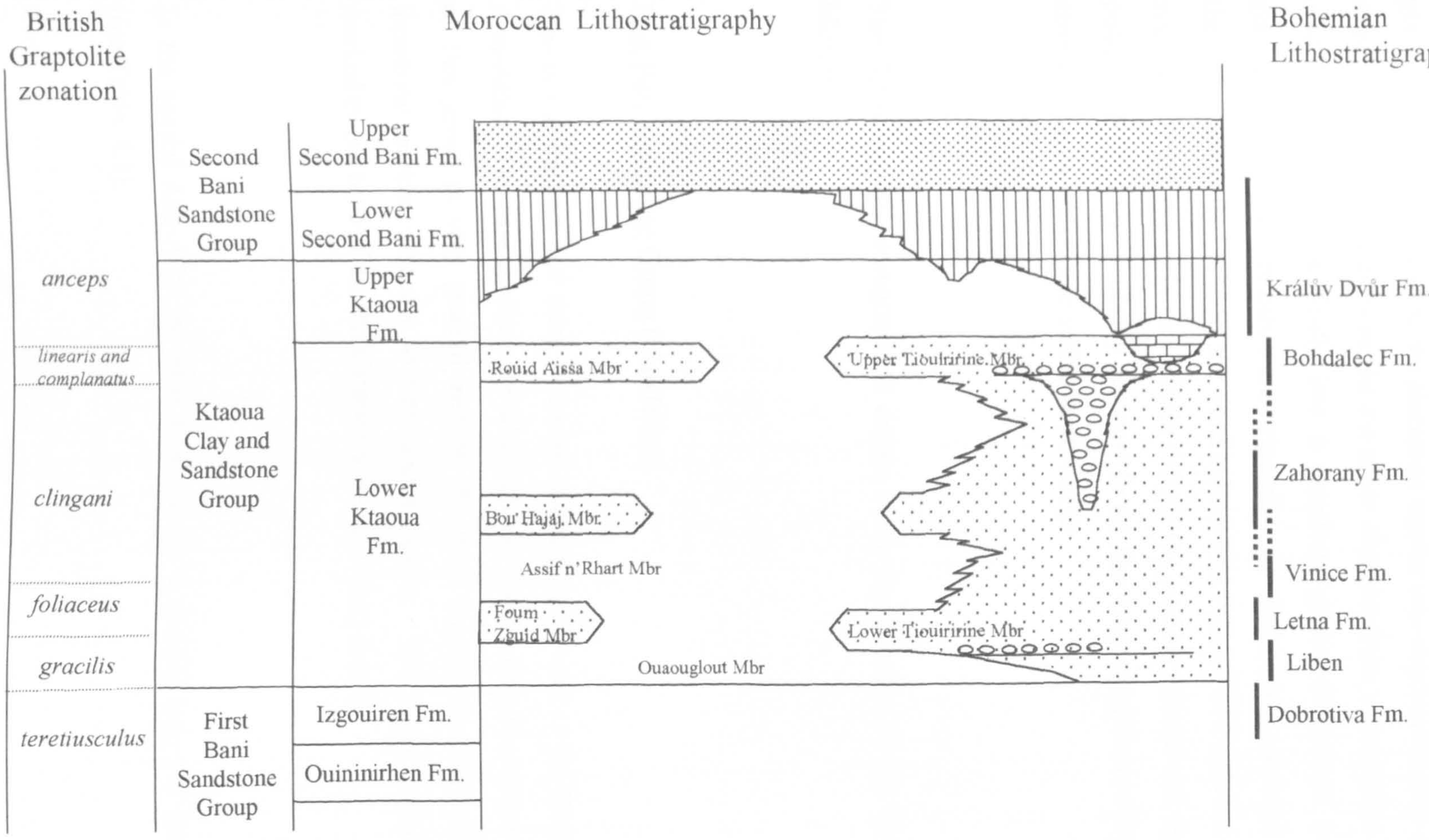
Text-Fig. 5.4. Map of Morocco showing the High and Anti Atlas regions of interest herein and the extent of Ordovician outcrop (from Destombes *et al.* 1985a).

During the Ordovician, Morocco was part of the northern margin of Gondwana and was situated at high latitudes. Indeed, during the Late Ordovician it was above the South Pole, (Scotese *et al.*, 1999). Destombes (1968a, 1968b, 1981) first recognized glacial sediments of late Ordovician age in the central Anti-Atlas. The glacial period

was thought to be from the Caradoc through into Wenlock times (Destombes *et al.* 1985, Frakes *et al.* 1992) or to have lasted for a maximum of only 0.5 to 2 million years (Brenchley *et al.* 1994, Paris *et al.* 1995 and Marshall *et al.* 1997). Isotopic evidence (e.g. Brenchley *et al.* 1994) indicates that in global terms, the glaciation was restricted to the early part of the latest Ordovician Hirnantian Stage. However, detailed study of successions in Morocco by Hamoumi (1988, 1994, 1999) have provided evidence to suggest that glacial processes had begun there as early as Llandeilian-Caradoc boundary and, through progressive advances and retreats of the ice cap, lasted into the early Silurian. The northern margin of Gondwana is postulated to have been a fjord-like environment with continual changes in sediment input and sea level from shifting, land based glaciers (Hamoumi 1999). Late Ordovician sedimentation occurred under the combined action of glacial and local processes in two shallow epeiric seas separated land: the Mesetian Basin and the Atalasic Basin.

Destombes *et al.* (1985a) outlined the stratigraphical framework of the Moroccan Ordovician, including lithological units (see Tables 5.1 and 5.2 and Text-Fig. 5.3). These units are not continuous across the region. At Tachila in western Morocco three lithostratigraphical units are present: the Lower Ktaoua Formation (lower to middle Caradoc), Rouid Aissa Formation (upper Caradoc) and the 2nd Bani Formation (upper Ashgill). Further to the east in the central Anti-Atlas, at Assif n'Rhart mountain some 50km NE of Zagora city, only the 2nd Bani Formation and Ktaoua Group are present. This succession rests on the First Bani Group of supposed Llandeilian age and is overlain by Silurian graptolite bearing siltstones, representing a sea level high after the late Ashgill glacially induced sea level low.

Destombes *et al.* (1985a) interpreted the Ordovician deposits as part of a transgressive-regressive marine cycle driven by the isostatic movements associated with magmatic activity in Tremadoc and Arenig times. The subsiding basin with land to the south allowed the accumulation of thick Llanvirn deposits. A regression during the Llandeilian Age gave way to localised transgressive pulses in the Caradoc Epoch. The bioturbated horizons in the upper Ashgill indicate a marine regression with glacial activity, centred on the Sahara, characterising the Second Bani Formation and later deposits in Morocco.



Text-Fig. 5.5. Lithostratigraphical units of Morocco, showing approximate Bohemian equivalent formations and British graptolite zonations for reference (based on Destombes 1985b).

Hamoumi (1999) interpreted Morocco's Gondwana margin in terms of tidally influenced fjords and deltas and not tideless epeiric seas, as previously thought. Hamoumi argued that uplift and the development of an ice cap in the latest Llandeilian/earliest Caradoc, created a marine outwash fjord adjacent to a temperate glacier. During the Caradoc the glaciation regime was characterized by a series of ice front retreats and advances as the ice cover changed from a temperate glacier into a cold based glacier and finally into a temperate glacier (Hamoumi 1999). These glacial advances and retreats were responsible for the eustatic sea level changes. At the end of the early Caradoc, the fjord system had evolved into a fluvial and estuarine system. During the early and middle Ashgill the cooling climate and development of polar conditions was probably responsible for the long stagnation of the glacier and absence of melt waters and sediment discharge.

The following lithostratigraphical details cover the duration of the Marrolithinae in Morocco:

First Bani Sandstone Group (Llandeilian)

This is the thickest and most extensive fine sandstone unit in the Ordovician of the Anti-Atlas. The passage from the silty facies of the Tachilla Formation to sandstones of this group is very gradual and by the local appearance of a thin lumachellic limestone markers adjacent to ferruginous oolites. The upper boundary is clearly marked by the base of the thick argillites of the Ktaoua Group.

In the central Anti-Atlas the First Bani Group is divided into five lithological units (see Table. 5.1).

	Lithostratigraphy	Lithology
First Bani Group	Izgouirn (Izegguirène) Formation	sandstone and local white micaceous siltstones.
	Ouininirhen (Ouine-Inirne) Formation	massive sandstones and quartzites, poorly consolidated in the east.
	Igzert (Guezzart) Formation	quartzites and massive white and green sandstones.
	Bou-Zeroual Formation	dark ferruginous sandstones.
	Taddrist Formation	dark and white sandstones. Many ferruginous.

Table 5.1. Table showing the five lithostratigraphical units of the Moroccan First Bani Group, including a brief lithological description (based on Destombes *et al*, 1985a).

The formations become less distinct towards the east within the mass of the First Bani Group. The presence of *D. murchisoni* below the Taddrist Formation suggests a lower age for the group as Llandeilian. The age of the youngest beds is more subjective (see Destombes *et al.* 1985a, p. 195).

Ktaoua Clay and Sandstone Group (Caradoc to middle Ashgill)

This group is divided into three formations. The top of the group passes very gradually upwards into the variablly argillaceous sandstones of the lower Second Bani Group.

Lithostratigraphy			Lithology
Ktaoua clay and sand-stone Group	Upper Ktaoua Argillite Formation (early-mid Ashgill)		Grey-green sandy siltstones with numerous fossiliferous pelo-carbonate nodules, rare oolitic iron or phosphatic nodule horizons.
	Upper Tiouririne (east) and Rouid-Aissa [Er-Rwaidat] (west) sandstone Formations. (late Caradoc [to earliest Ashgill on correlation Fig]		Pink planar bedded sandstone sheets with conglomerate intercalations, becoming coarse to west and highly ferruginous locally with oolites (west). Above the conglomerates it consists of thick green micaceous sandstones with pelitic carbonate nodules. Dark micaceous sandstones with intercalations of lumachellic limestones or bluish silty limestones
	Lower Ktaoua (clay-sandstone) Formation (early-mid Caradoc)	Agadir-Tissinnt Siltstone Member	white silty shales grading upwards into dark green and black fine silty shales with thin sandstone beds in their upper part. Some beds pink and contain horizons of oolitic ironstone and pelo-carbonate nodules. Grading eastwards into sandstones with local conglomeratic lenses.
		Jbel Taberkat (south-east) or Bou-Hajaj [H'asi Taska] (west) Sandstone Member	locally developed above the siltstones of Assif n'Rhart.
		Assif n'Rhart Siltstone Member	fine sandstones, micaceous, grey siltstones with lenses of pelo-carbonate. Common oolitic horizons.
		Lower Sandstone Member of Tiouririne (east), Foum-Zguid (west)	calcareous sandstones (east), thick and coarse, ferruginous quartzites with cross-bedding (west).
		Ouaouglout Siltstone Member	siltstones with interbedded sandstones including fossiliferrous nodules.

Table 5.2. Lithology of the various formations in Morocco, Caradoc to middle Ashgill, based on Destombes *et al.* (1985a) who correlated the succession with that of the Prague Basin (Bohemia). The ages given herein are based on a more recent correlation of those units with the Anglo-Welsh chronostratigraphy (see Fortey et al. 2000, fig 34).

5.3.3 Perunica

The Ordovician succession of the Prague Basin was summarized by Štorch *et al.* (1999) and is typified by alternations of shaley and sandy facies. The distal parts of the shallow water sandstone facies reached the central depression of the basin although in general, this central area was characterized by black shales from the beginning of the Llanvirn (Šárka Fm.) until the earliest Ashgill (Bohdalec Fm.). Several ironstone horizons are present and are the basal markers for some lithostratigraphical units. Extensive Ordovician basalt volcanism began in the Arenig and persisted into early Ashgill. The Ordovician rocks, including the volcanic units are up to 2,500m thick.

5.3.4 Armorican and Iberian Peninsulas

The widespread (France, Iberia and Sardinia) Armorican Sandstone Formation marks the base of the Ordovician in the region (Álvaro *et al.* 1999). In Armorica, the Andouillé Formation (Llanvirn) is composed of siltstones and mudstones with interbedded volcanic units within the lower Llanvirn. The following formations are the lateral equivalents of the Andouillé Formation: the Moitiers d'allonnes, d'Urville and lower Mont de Besneville, Postolonnec, May and the Traveusot formations. The Saint Germain sur Ille Formation (Caradoc and Ashgill) is composed of sand and siltstone cycles. The lateral equivalents of this are the upper Mont de Besneville, Sangsurinére and the Pélites à fragment Formations, Grés de kermeur Formation and the Chatellier and Radian Formations.

The proximity of France to Iberia during the Ordovician is reflected in the similarities of sequences and facies relationships (Young 1988). The Postolonnec Formation is contemporaneous with the Carregueira Formation (Lower Caradoc), which is composed of dark mudstones with pyritic nodules. The Louredo and Cabeço do Peão are laterally equivalent formations in the Caradoc. Both are composed of mudstones

with intercalated sandstones, the lower ones of which are bioturbated and grade up into micaceous bioturbated mudstones. The rest of the formation is made up of cycles of sandstones and mudstones. The Porto de Santa Anna Formation and its equivalent Rosan Formation (Pusgillian to Rawtheyan) are a mixture of volcanic horizons and silicified sandstone beds which were probably originally carbonates.

5.3.5 Sardinia

For much of the early Ordovician Sardinia was possibly above sea level (indicated by the Sardic unconformity). Loi and Dabard (1999) proposed that it was geographically close to Armorica due to the presence of siliceous-argillaceous nodules in both the Portixeddu and Postolonnec formations. These storm deposited shelf mudstones and siltstone are directly above the widespread Armorican Sandstone Formation. The Armorican Sandstone Formation *sensu lato* is found throughout Iberia, France, Sardinia, the Pyrenees and the Carnic Alps (see Hammann & Leone 1997, Romano 1982 and Robardet *et al.* 1980). Loi and Dabard (1999) suggested the presence of two basins of deposition in Sardinia based on the presence of Gondwanan detrital zircons.

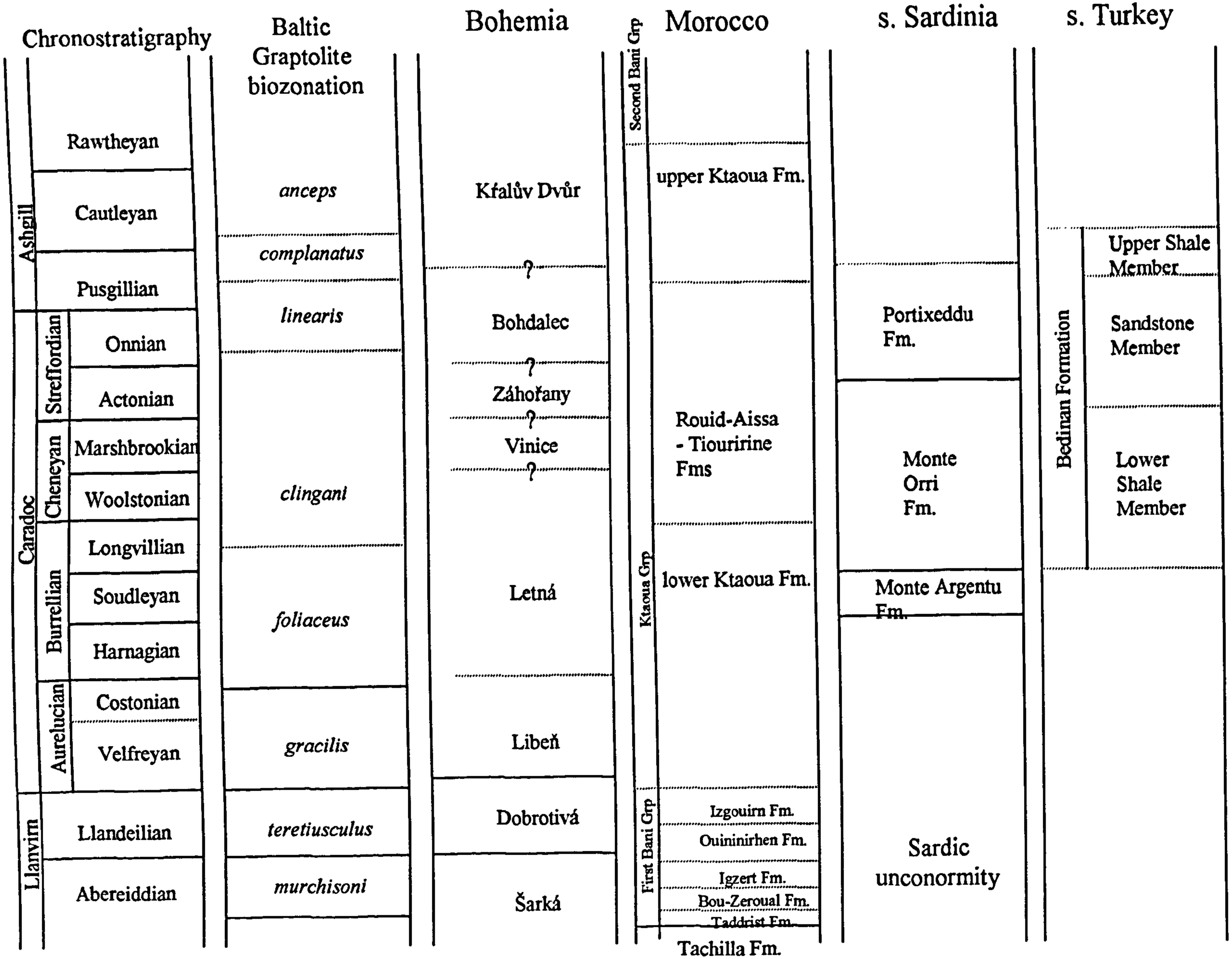
5.3.6 Turkey

Dean *et al.* (2000) drew attention to the difference in lithologies between Northern and Southern Turkey. The Aydos Formation (Arenig) comprise massive shallow marine quartzites and is similar to the Armorican Quartzite, which extends from Brittany to Iberia and may be represented in eastern Newfoundland (Dean, 1976). Alternating flysch like successions (Arenig) extend from southern France, to the Zap valley, in southern Turkey (Dean, 1980) and extend further east into southern western China (Zhou, Dean and Lou, 1998). Conspicuous differences between the northern and southern developments of the Ordovician rocks are seen in the Llanvirn and later series. Although well represented in the Middle East, especially Saudi Arabia (El-Khayal and Romano, 1985), the Llanvirn is reported from only one faulted section near Silifke, on the south coast of Turkey (Sarmiento et al., 1999). The Llandeilian is as yet unknown from both Taurides and Border Folds, where the Bedinan Formation (Caradoc-Ashgill) is separated from Arenig or older rocks by a regional disconformity

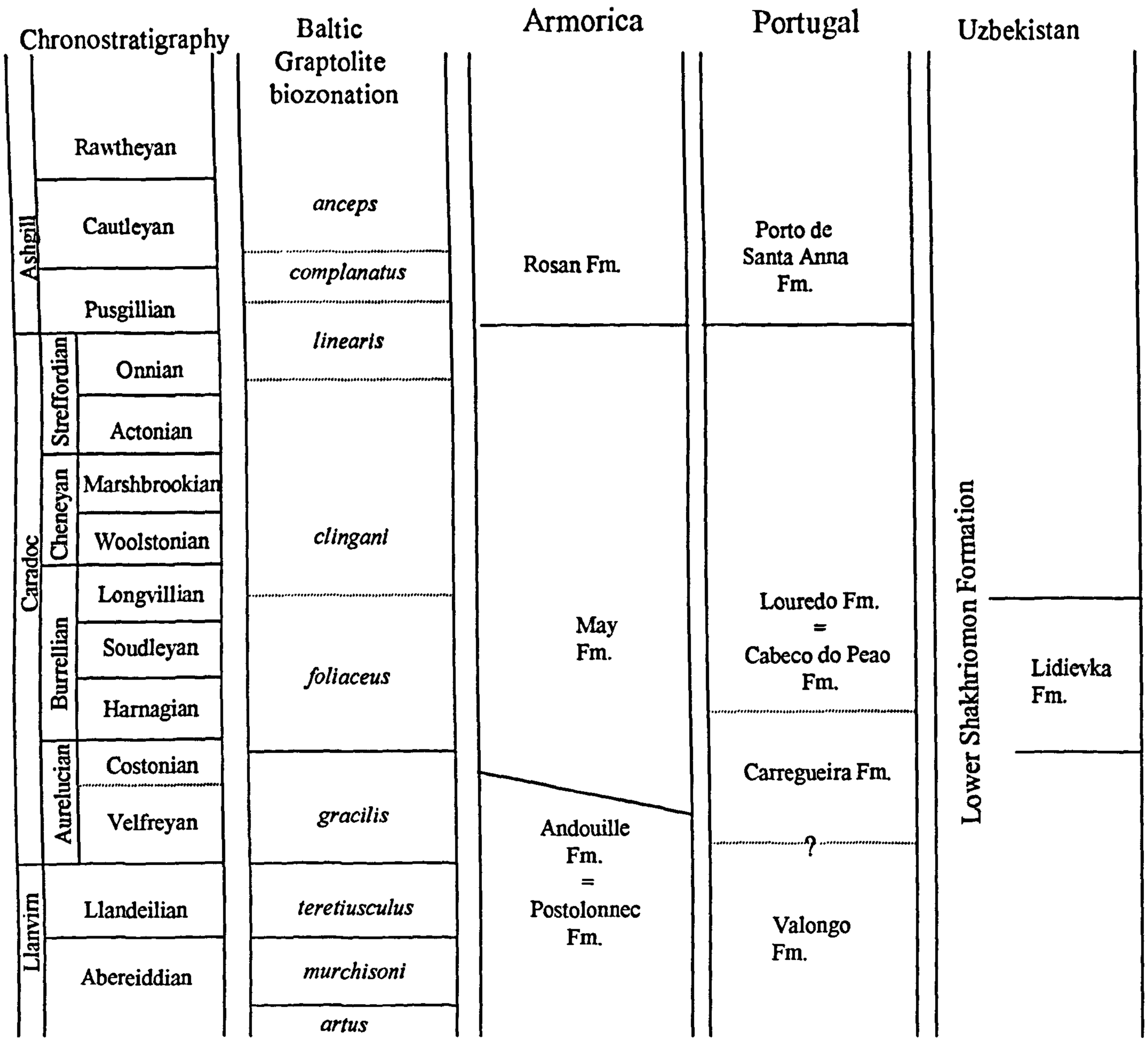
(Dean *et al.*, 1981). The Bedinan Formation is overlain by the lower Ashgill Şort Tepe Formation (Dean and Monod, 1990). The Bedinan Formation is composed of three Members; the Lower Shale Member, the Sandstone Member with no fossils and the Upper Shale Member (1983) Dean.

5.3.7 Venezuela

The position of South America has in the past been widely different but concensus now puts the part of the craton where Venezuela is situated now at high latitude. although the stratigraphical evidence is lacking for the relative ages of the Venezuelan *Reuscholithus*

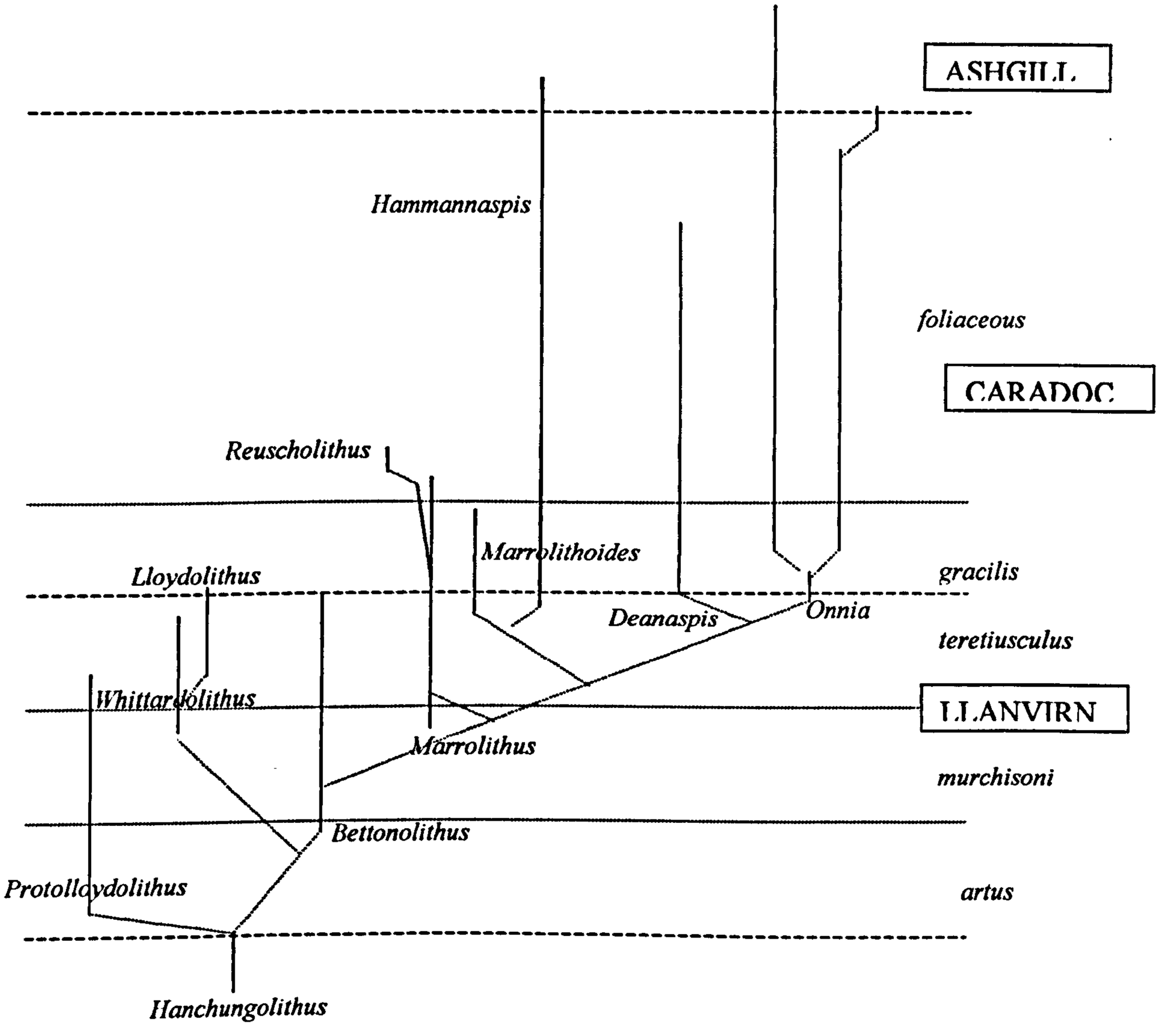


Text-Fig. 5.6. World correlation charts, based on Fortey *et al.* (2000), Alvaro *et al.* (1999), Young (1988), Romano (1982), Dean (1980), Destombes (1985), Williams *et al.* (1972).


Chronostratigraphy
Baltic Graptolite biozonation
Armorica
Portugal
Uzbekistan
Ashgill
Caradoc
Llanvirn
Streffordian
Cheneyan
Burrellian
Aurelucian
Rawtheyan
Cautleyan
Pusgillian
Onnian
Actonian
Marshbrookian
Woolstonian
Longvillian
Soudleyan
Harnagian
Costonian
Velfreyan
Llandeilian
Abereiddian
anceps
complanatus
linearis
clingani
foliaceus
gracilis
teretiusculus
murchisoni
artus
Rosan Fm.
May Fm.
Andouille Fm. = Postolonnec Fm.
Porto de Santa Anna Fm.
Louredo Fm. = Cabeco do Peao Fm.
Carregueira Fm.
?
Valongo Fm.
Lower Shakhriomon Formation
Lidievka Fm.

6 Palaeogeographical history of the Marrolithinae

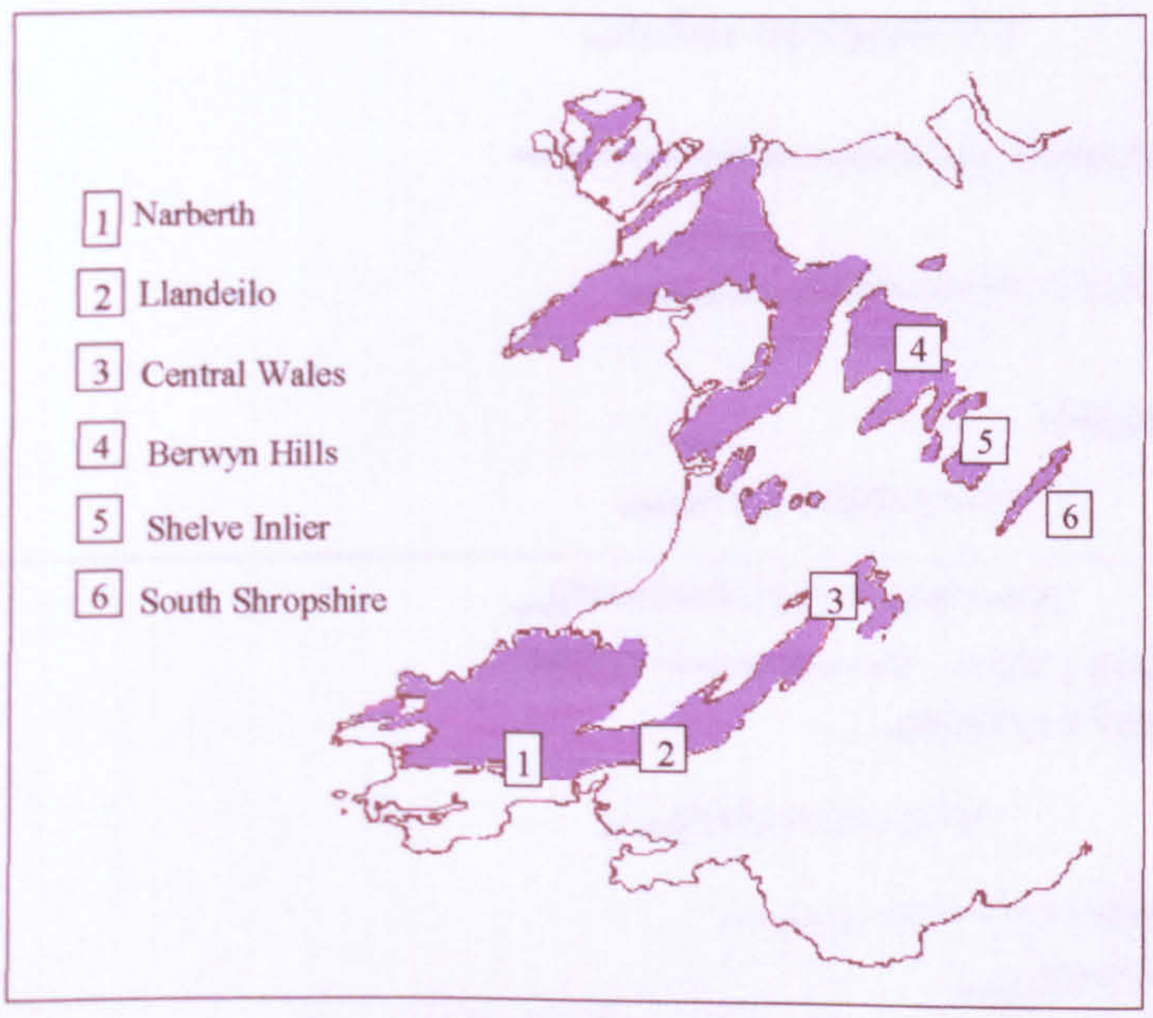
The distribution of the Marrolithinae can now be documented and analysed in the light of the substantial taxonomic revisions detailed in Chapter 4 and the generic relationships are sketched out in Text-Fig. 6.1.



Text-Fig. 6.1. Systematic phylogenetic relationships of the Marrolithinea as described herein.

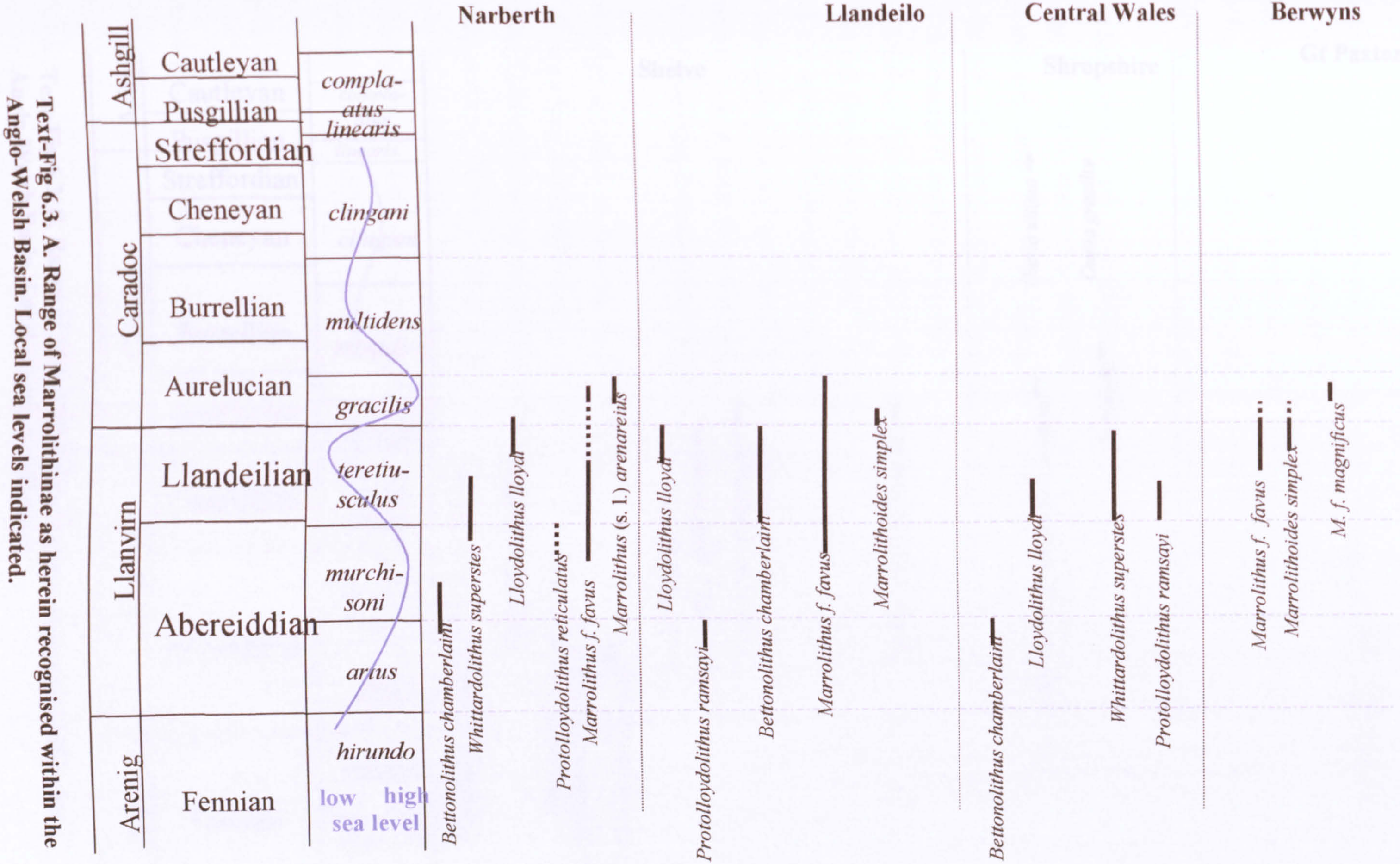
6.1 Avalonia

The large number of marrolithine species described from the Anglo-Welsh area is testament both to its history of being intensely studied and to the isolation of the evolving fauna within the Welsh basin from those of the major plates. Marrolithinae taxa have been used as zonal fossils (e. g. Bancroft 1933, 1949; Williams 1948 and Bettley *et al.* 2001) to aid correlation between Anglo-Welsh successions but the typological approach adopted in the past has restricted the usefulness of some species. The use of local names for the same formation has also caused confusion in the past however, recent work by Rushton *et al.* (2000), Fortey *et al.* (2000), Bettley *et al.* (2001) and Bowdler-Hicks *et al.* (2002) has clarified both lithological and biostratigraphical correlations. Text-Fig. 6.2 shows the six main areas that contain members of the Marrolithinae.



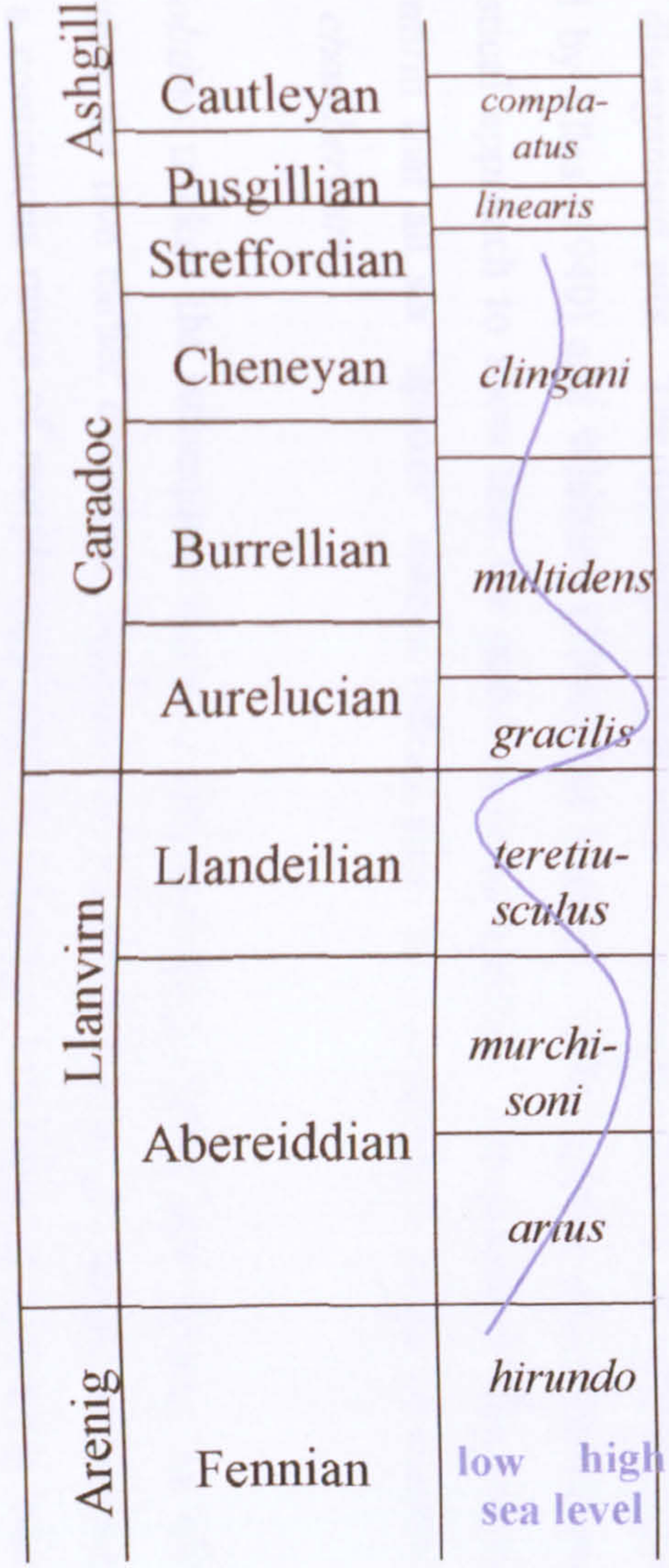
Text-Fig. 6.2. Map showing Ordovician outcrops and main locations of the Marrolithinae in Wales and the Welsh Borders.

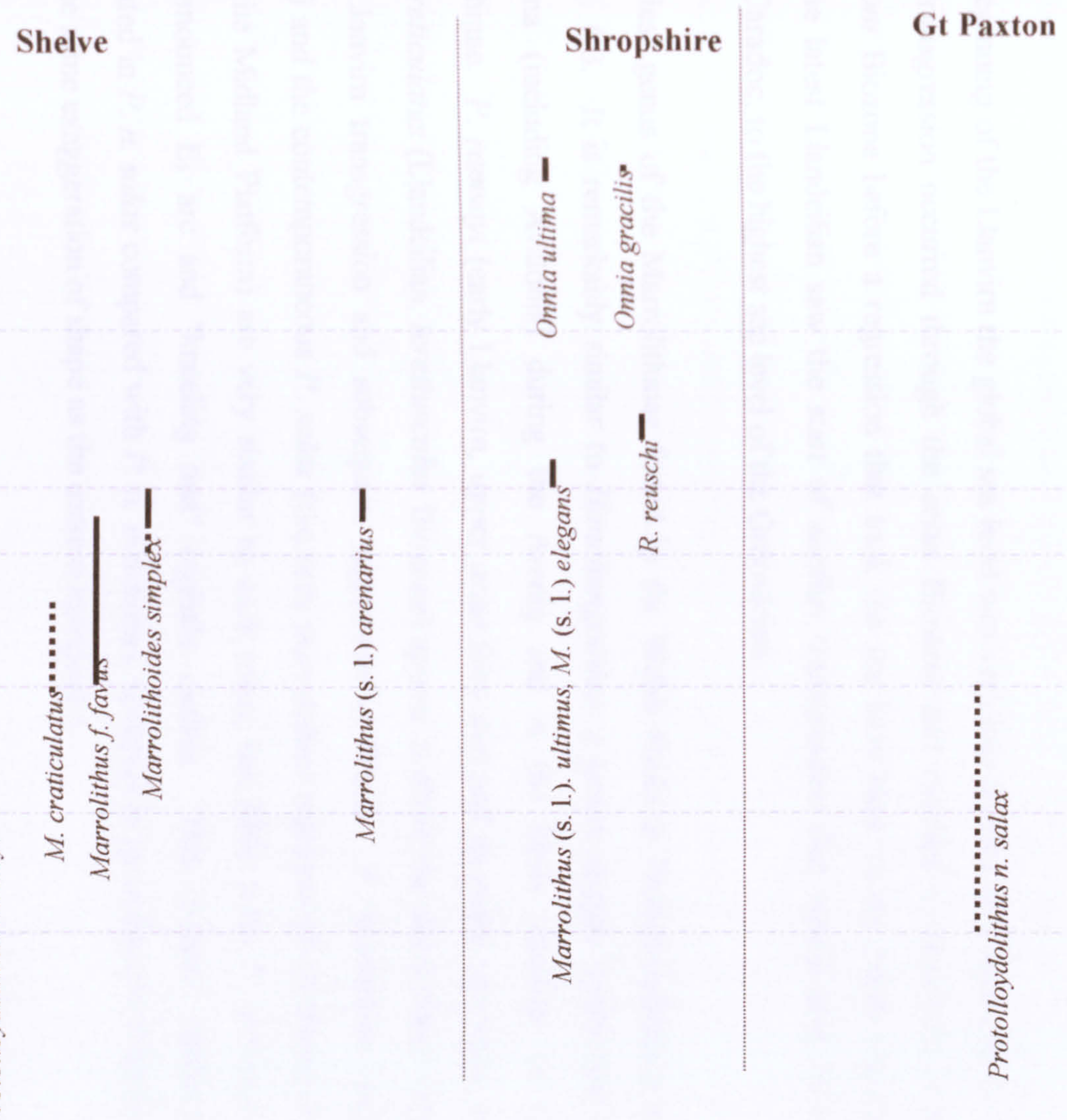
Throughout the Ordovician Avalonia was subjected to sporadic magmatic activity. This affected the sedimentation rate, sea level and possibly even influenced speciation (see Botting 2002).



Text-Fig 6.3. A. Range of Marrolithinae as herein recognised within the Anglo-Welsh Basin. Local sea levels indicated.

Text-Fig 6.3. B. Range of Marrolithinae as herein recognised within the Anglo-Welsh Basin. Local sea levels indicated.





6.1.1 Llanvirn

At the beginning of the Llanvirn the global sea level was very low (Fortey & Cocks 1986). A marine transgression occurred through the *artus* Biozone and reached a maximum in the *murchisoni* Biozone before a regression that took the sea level back to the initial Llanvirn level. The latest Llandeilian saw the start of another transgression that would lead, in the earliest Caradoc, to the highest sea level of the Ordovician.

The earliest genus of the Marrolithinae found in the Welsh Basin is *Protolloydolithus* see Text-Fig. 6.3. It is remarkably similar to *Hanchungolithus* a genus already established in Gondwana (including Avalonia) during the Arenig and is the likely ancestor of the Marrolithinae. *P. ramsayi* (early Llanvirn, upper *artus* Biozone) and its junior synonym, the later *P. reticulatus* (Llandeilian, *teretiusculus* Biozone) appear at about the same water depth of the Llanvirn transgression and subsequent regression in Wales. *P. neintianus* (early Llanvirn) and the contemporaneous *P. salax* (the only marrolithine represented on the eastern side of the Midland Platform) are very similar to each other, but differ from *P. ramsayi* in their pronounced E_1 arc and "kneeling mat" cephalic outline. This cephalic outline is exaggerated in *P. n. salax* compared with *P. n. neintianus*, however in juveniles of the latter it shows the same exaggeration of shape as the eastern subspecies.

Bettonolithus appeared in Avalonia during the Llanvirn transgression (see Text-Fig. 6.1, 3, 7A). It has a long stratigraphical range extending from the middle Abereiddian Stage to the top of the Llanvirn Series and appeared in central Wales slightly earlier than in the Shelve and Llandeilo districts. It has a highly organised pit pattern with only a small area posteriorly showing disorganised pits. The typological approach to taxonomy led to six species being described by Elles (1940) and Whittard (1956) but Hughes (1971) used a population-based and statistical approach to show that the genus in monospecific. The results of the present study confirm that all six "species" simply reflect parts of a continuous range of variation within *B. chamberlaini*.

Whittardolithus tracked the subsequent marine regression from Shelve into Wales. As with *Bettonolithus* the five earlier described "species" of *Whittardolithus* are simply overlapping parts of a continuous range of morphology and pit numbers. There is a decreasing trend through time in the number of small randomly distributed pits posteriorly, used previously to

distinguish each "species" (Whittard 1956; Hughes 1971). This progression to ordered pit patterns is a recurring feature within the trinucleids (Hughes *et al.* 1975, p. 590).

There are strong morphological similarities between *Bettonolithus* and *Whittardolithus* such as the subrounded cephalic outline, flat fringe surface with negligable anterior arch, increased pit width and ordered pit pattern in E_1 and I_1 arcs, distinct first internal list and some degree of pit irregularity poateriorly. These similarities may help explain why "*Cryptolithus*" *superstes* (Whittard, 1956) was first placed in *Bettonolithus* [then *Bettonia*] by Hughes (1971) and then moved to *Whittardolithus* by Hughes *et al.* (1975). Following the synonymies proposed herein, *Whittardolithus superstes* (Whittard, 1956) becomes the type species for this monospecific genus.

Lloydolithus is another monospecific genus showing considerable variation within the pit ranges of all arcs and like *Protollyodolithus*, *Bettonolithus* and *Whittardolithus* it has some degree of pit irregularity posteriorly. All four genera occur in deep water deposits. *Lloydolithus* also occurs in high subtidal sand/siltstone deposits associated with the major transgression that began near the end of the Llandeilian (Wilcox and Lockley 1981). These deposits also contain specimens of *Marrolithus favus favus* (see below). *Lloydolithus* is the only genus out of the four to persist into the lowest Caradoc.

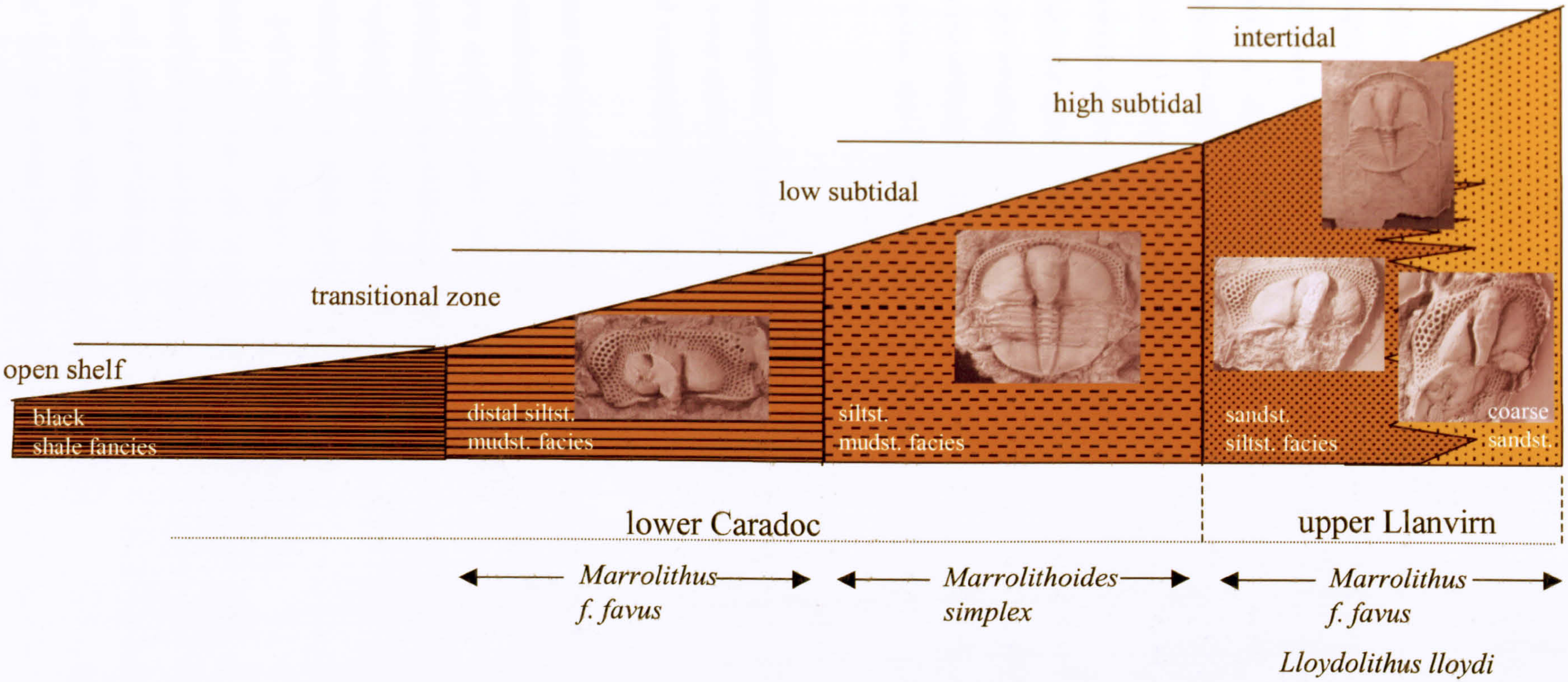
The genus *Marrolithus* appeared at the start of the regression near the end of the middle Llanvirn Series. Twelve species and subspecies of this genus have been described from Avalonia, with some used as zonal indices (see Bettley *et al.* 2001, for the most recent usage).

Marrolithus craticulatus is the only marrolithine apart from *Protolloydolithus* that possesses swollen pits in the E arc. It is restricted to the lower Llandeilian Stage of Shelve.

Marrolithus favus favus is herein redefined to encompass the six taxa established by Williams (1948) in the Llandeilo and Whittard (1956) working in the Shelve area. All these supposed species and subspecies show an overlapping range in variation seen in the number of pits affected by the fringe inflation, the elevation of inflation, number of pits in arcs, fringe outline, overall size, presence of arcs and the shape and size of the inflations on the fringes. These differences are a reflection of the variation of a single species enhanced by differential preservation of specimens.

A detailed palaeoecological study by Wilcox and Lockley (1981) of the near shore environments of the Llandeilo area demonstrated the faunal changes associated with the late Llanvirn and early Caradoc marine transgression. The chronostratigraphical scheme that they employed was that advocated by Williams *et al.* (1972) and has been superceded by that of Fortey *et al.* (1995, see also 2000). A picture of shifting populations tracking particular environmental parameters is now emerging and is made clearer with the synonymy of the numerous *Marrolithus* "subspecies" described above. The late Llanvirn, near shore, sandy-silt facies contain *Lloydolithus* and *Marrolithus f. favus* [= *Marrolithus inflatus inflatus* and *M. i. maturus* of earlier usage] (see Text-Fig. 6.4). As marine conditions became deeper in the early Caradoc, another marrolithine genus, *Marrolithoides*, replaced the earlier forms and persisted there until the water depth in the near-shore transitional zone became deeper (greater than the normal wave base) when *M. f. favus* [= *Marrolithus f. favus* and *M. f. moderatus*] returned in the now distal silty mud deposits. During its absence from the Llandeilo district *M. favus* was present in Shelve and the Berwyns. Its absence from Llandeilo may be due to the local environment being unsuitable and it followed its particular niche along the shelf to Shelve and further north to the Berwyn Hills.

During the late Llandeilian, *Marrolithus favus favus* extended its range from Narberth in the southwest to what are now the Berwyn Hills to the north.



Text-Fig. 6.4. Diagram showing the inferred palaeoenvironmental setting for the Llandeilo area. The Marrolithine species are superimposed and suggest environmental preferences, (after Wilcox and Lockley (1981)).

6.1.2 Caradoc

As is noted above the deepening waters around Llandeilo brought an influx of individuals of *Marrolithoides* during the earliest Aurelucian; a genus with a distinct narrow fringe, large genal lobes, a low number of I arcs and pits and slight inflation of the fringe posterolaterally. Four species and subspecies have been named (Williams 1948; Whittard 1956); three being found together in Wales and two in Shelve. Although Addison (1974) compared population samples and suggested that they all might be a single species, Wilcox and Lockley (1981) argued that *M. simplex* and *M. anomalis* could be differentiated and retained them as zonal fossils. Wilcox and Lockley's proportion charts for *Marrolithoides simplex* and *M. anomalis* show proportional variation in the percentage of each species within the samples and it is here suggested that the supposed specific differences between the two "species" are partly due to preservation in different lithologies (*M. anomalis* was identified from limestone beds) and partly to adaptions to the different environments which produced the different lithologies. *M. anomalis* and *M. arcuatus* (the Shelve representative) are here considered synonymous with *M. simplex*.

Marrolithus favus magnificus typified by extreme fringe inflation is found only in the Aurelucian of the Berwyns and is associated with *Marrolithus f. favus*. It is possible that this extreme form is a local variant of the type species.

Some marrolithines from the Aurelucian Substage show low fringe inflations containing no I_3 arc pits and lower numbers of I_2 pits, described by Whittard's (1956) as *Marrolithus arenarius*, *M. bilinearis* and *M. scalpriformis* from the *gracilis* Biozone of the Shelve area. *M. arenarius* and *M. bilinearis* are found together in most locations and are extremely similar and *M. bilinearis* is synonymised here within *M. arenarius*. *Marrolithus ultimus* [the type species of *Costonia*] shows clear radial rows, few F pits and few irregular pits posteriorly. *Marrolithus elegans* [=*Costonia elegans* Dean, 1960] conversely, shows poor radial alignment, a high number of F pits and disorganised pits posteriorly. During this study it became evident that there has been an assumption that *M.* (s. l.) *ultimus* and *M* (s. l.) *elegans* are only found south and north of Cardington Hill, respectively, which has led to numerous specimens in museum collections being misidentified. Both species are widely distributed throughout Shropshire. *M. arenarius*, *M. ultimus* and *M. elegans* all show the characteristic diagnostic features of *Marrolithus*, fringe inflation of at least two arcs, prominent girder at the

anterior, ordered pit arrangment to posterior area. The cladistic analysis (see Section 3.3) however, showed discrepency in the placing of these three species and therefore they are placed in *Marrolithus* (sensu lato) to reflect this.

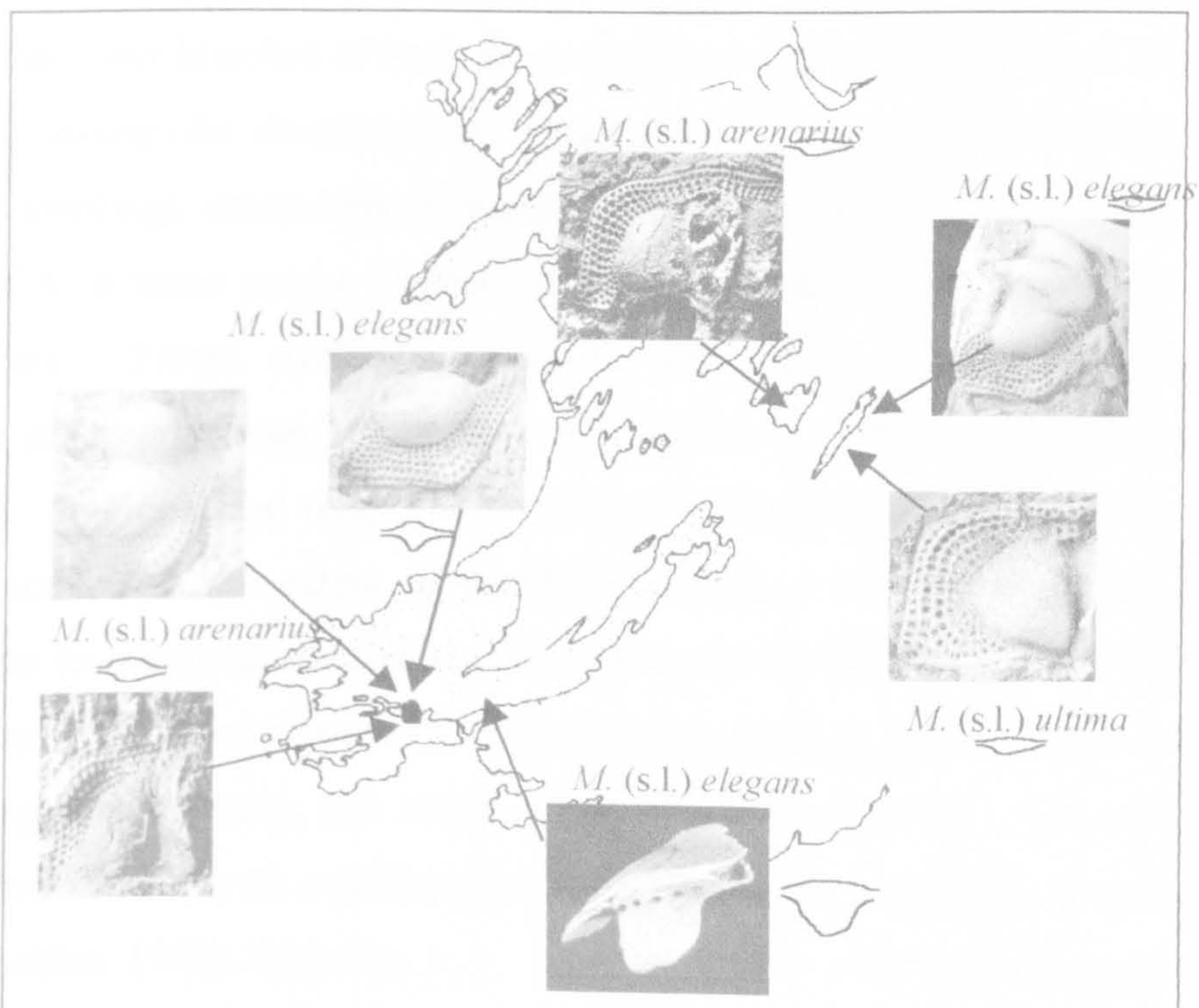
Marrolithus (sensu lato) *arenarius* and *M.* (s. l.) *elegans* are also found in South Wales and temporal and geographical variations in fringe morphology can be seen within the two species. At Narberth, in South Wales, *M. arenarius* shows greater fringe inflation than in the east (Shelve) (see Text-Fig. 6.5). Bettley (unpublished PhD. thesis 1998) placed all these Welsh forms in *Costonia arenaria* and assigned stratigraphically younger material from South Wales, showing increased pit counts in internal arcs and more localised, pronounced inflations to a new subspecies *C. arenaria addisoni* [now = *Marrolithus* (s. l.) *elegans*]. There is a reduction in fringe inflation from west to east in *M.* (s. l.) *arenarius* and *M.* (s. l.) *elegans* (see Text-Fig. 6.5). Another trend observed from west to east is the introduction of E_2 pits frontally, this is seen in *M.* (s. l.) *elegans* and the contemporaneous Shelve species *M.* (s. l.) *ultimus* also shows this feature in about half of the specimens in any one sample. Bettley *et al.* (2001) used *Marrolithus bilinearis* [now = *M.* (s. l.) *arenarius*] and *Costonia arenaria* [now = *M.* (s. l.) *arenarius*] as biozonal species for the upper Aurelucian Stage based on their composite standard ranges.

Reuscholithus reuschi is stratigraphically the highest marrolithine in the lower Caradoc of the Welsh Basin and shows a higher degree of pit irregularity than all other marrolithines. There are similarities to *M.* (s. l.) *elegans* such as the large area of irregular pits posteriorly, cephalic outline and glabella shape. This may suggest a possible close relationship (see Text-Fig. 6.1).

The Cryptolithinae appeared in the Anglo-Welsh basin at the same time as *Reuscholithus*. The latter disappeared from the area whislt the cryptolithines became widespread during the absence of the Marrolithines (see Bowdler-Hicks *et al.* 2002).

After an absence from the Basin marrolithines repopulated Avalonia in the Streffordian (late Caradoc) and early Pusgillian (earliest Ashgill) with species of *Onnia*, a genus of periGondwanan origin. Owen & Ingham (1988) carried out a detailed review of *Onnia* in the Caradoc of Shropshire. Four species or subspecies *Onnia* occur in the type Onnian Substage, and are used as biozonal indicators. *O. ultima cobboldi* [= *O. superba cobboldi* of earlier usage] was the first Onnian immigrant and possessed a highly organised fringe pit

arrangement with swollen I_1 and I_2 arc pits. This was then replaced by *O. ultima creta* [= *O. s. creta*] containing significantly lower pit counts and large I_1 pits and elevated I_1 and I_2 arcs. The unrelated *Omnia gracilis*, with high pit counts in all arcs, especially E_1 and swollen I_1 and I_2 pits, replaced *O. u. creta* having already established itself in Shropshire in the Actonian. *Onnia ultima superba* [= *O. superba superba*] replaced *O. gracilis*. This shows pit counts similar to *O. s. cobboldi* in most arcs but a less convex curvature of the fringe and a higher mean and range of E_1 pits. There is a stratigraphical variation in the number of E1 pits from lower counts in the early *Onnia ultima superba* Local Range Zone compared to higher pit counts in the late *Onnia ultima superba* Local Range Zone. The only Marrolithines represented in northern England are *Onnia gracilis*, the younger *O. pusgillensis* and rare *O. u. superba* specimens. These were the last representatives of the Marrolithinae within Avalonia and had disappeared by the middle of the Pusgillian Substage.

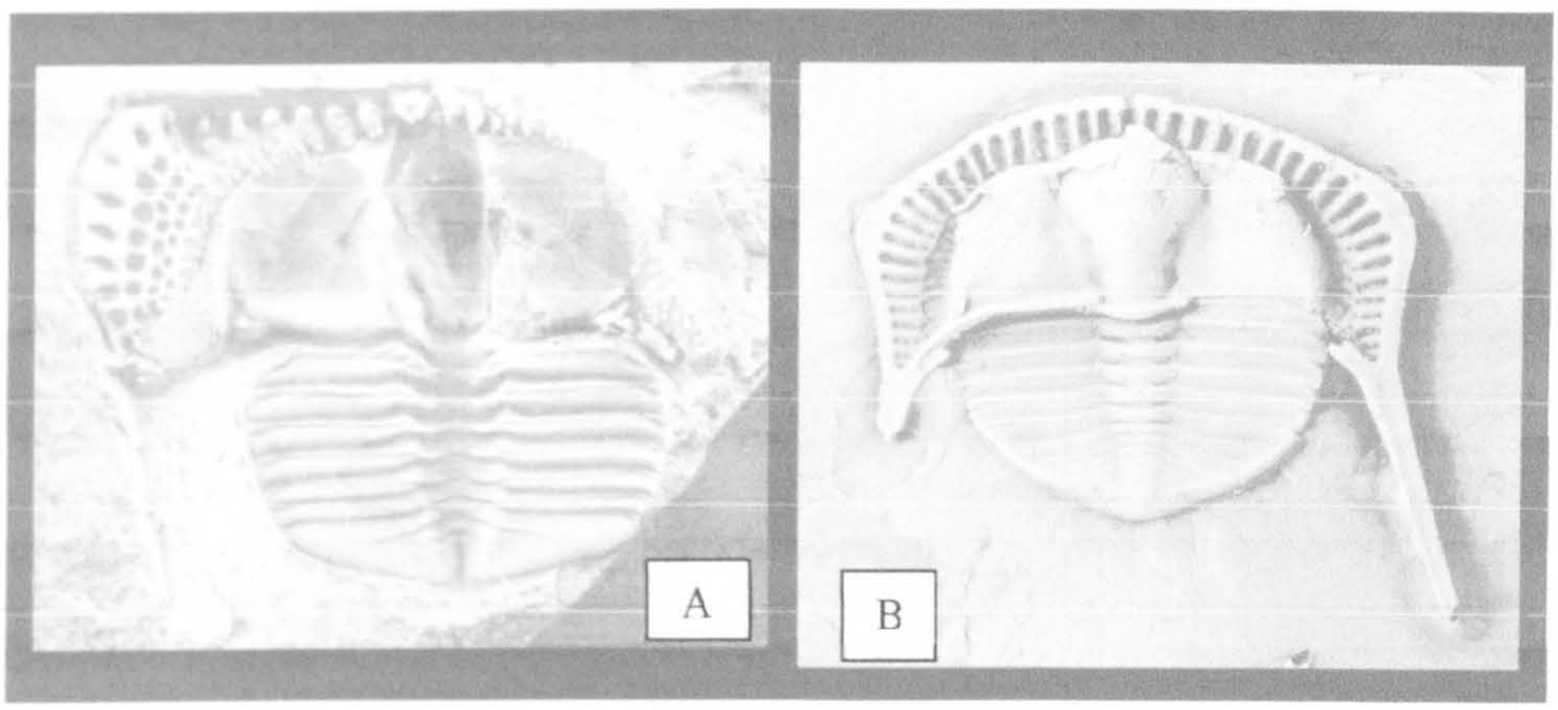


Text-Fig. 6.5. Variation in fringe inflations between *Marrolithus (s. l.) ultimus*, *Marrolithus (s. l.) arenarius* and *Marrolithus (s. l.) elegans*.

6.1.3 Additional comments on selected Avalonian taxa

Avalonia had probably rifted from the Gondwanan margin by the time of first appearance of *Protolloydolithus*, in the early Abereiddian Substage. The northward drift of Avalonia progressively isolated it from the shelf area of Gondwana and as it travelled northwards the temperature increased. According to Christiansen and Stouge (1999), the major ocean currents were in a clockwise gyre around the rifted plate. Tectonic and magmatic activity and eustatic sea level changes constantly affected the local sea levels. These transgressive and regressive cycles in Avalonia mirrored the global sea level (Fortey and Owens 1987) and influenced the distribution of the marrolithines.

Marrolithus first appeared in Avalonia before other Gondwanan areas. *Marrolithus craticulatus* shows larger E_1 and I_1 pits and radial alignment, features similar to the earlier *Bettonolithus* and the lower lamellae of both show a distinct girder along the entire fringe and some first internal pseudogirder development. *Marrolithus* was the only Marrolithine genus to "exploit" fringe swellings extensively although other genera such as *Marrolithoides* and *Hammannaspis* and to a lesser extent *Deanaspis* and *Onnia* show slight inflations generally restricted to one arc. Fringe swellings were not confined to the Marrolithinae, some Trinucleine genera possesed fringe inflations e. g. *Telaeomarrolithus* and *Ningkianolithus* (see Text-Fig. 6.6). Regional and temporal variations in fringe swelling within *Marrolithus favus* were considerable but the extent of the fringe inflation may not have been directly related to adaptation to particular substrates. The long stratigraphical range of *Marrolithus favus* (from the base of the Llandeilian to the Aurelucian Substages) suggests that it was well adapted to changing environments and could track its prefered niche. The stasis in the morphology of *Marrolithus* may be a reflection of the changing environment that included sea level fluctation (Sheldon 1990) Text-Fig. 6.3. *Marrolithoides*, was contemporaneous with *Marrolithus* but must have occupied a slightly different niche as the two genera are rarely found together.



Text-Fig. 6.6 A. *Ningkianolithus*, x4 and B. *Telaeomarrolithus*, x4.

Reuscholithus is also found in Venezuela, which was at a similar latitude to Avalonia in the early Caradoc (Cocks, 1999). The Venezuelan material is unfortuneately poorly constrained stratigraphically and the direction of movement of the genus is therefore unknown. The loss of radial alignment of pits in *Reuscholithus* may have been an adaptation to the ever increasing water depth. It was replaced by another trinucleid subfamily showing even more pit irregularity, the Cryptolithinae (see Bowdler-Hicks *et al.* 2002) and from the Burrellian to the middle Streffordian substages Avalonia has no recorded Marrolithinae. During the Streffordian the Cryptolithinae were abruptly replaced by the peri-Gondwanan immigrant, *Onnia*. This genus came into Avalonia in pulses starting with *Onnia gracilis* in the Actonian followed by a subspecies of the other *Onnia* lineage, *O. ultima* at the beginning of the Onnian. The rapid reappearance and subsequent disappearance of *O. gracilis* in the mid Onnian with only minimal co-occurrence with the preceeding and succeeding *O. ultima* subspecies strongly suggest that the two stocks had markedly different niches. The last *Onnia* in Avalonia (in Northern England) *O. pusgillensis* was probably a derivative of *O. gracilis* resulting from a decrease in pit numbers and an increase pit widths; a pattern seen in Morocco but to a lesser extent. Possibly because of increasing water depth, *Onnia* and therefore the Marrolithinae is not recorded from middle Pusgillian onwards on Avalonia.

The appearance of *Onnia* in the Actonian of the Anglo-Welsh area coincided with the appearance of another trinucleid, the trinucleine *Tretaspis* (see Owen and Ingham 1988). This

genus diversified rapidly in the early Ashgill (e.g. see Ingham 1970, Thomas *et al.* 1984) and thrived until the end of the Rawtheyan.

6.2 Morocco

Morocco was situated near the South Pole during much of the Ordovician (Cocks 2000) on the Iapetan margin of Gondwana. The major glaciation centred on the Sahara was relatively near to this part of the margin and would have influenced sediment deposition and sea level changes (isostatic and eustatic). The Llandeilian as used by Destombes (1985a) equals the Llandeilian *sensu* Fortey *et al.* (1995, 2000). The top of the Llandeilian corresponds to the top of the First Bani Group.

6.2.1 Llanvirn

Marrolithus favus favus is found in iron rich fine silt and sandstones from the upper Llandeilian Substage Izgouirn Formation and possibly from the Bou-Zeroual Formation of the First Bani Group. The Moroccan specimens occur with *Microparia* (*Degamella*) *princeps princeps* (Barrande) which is indictive of the Dobrotiva Formation of Bohemia and would therefore suggest a Llandeilian age.

Hammannaspis also appears in Morocco much earlier than other areas. The lithology of the deposits in which it occurs is mainly iron rich sandstones and in Perunica it is first found in iron ore unit at the base of the Vinice formation.

6.2.2 Caradoc and Ashgill

Species of both *Deanaspis* and *Onnia* are found at the base of the Caradoc. *Deanaspis goldfussii goldfussii*, an immigrant from Perunica, ranges through the lower half of the Caradoc but possibly never in great numbers. *Onnia* shows a stratigraphical progression to lower pit counts, increased pit widths of arcs I_1 and I_2 and slight posterior fringe inflations and remained in the region until the Ashgill when the water depth probably became too great.

6.2.3 Palaeogeography of Morocco

Morocco was the most southerly area populated by the marrolithines. The migration of the peri-Gondwanan *Marrolithus favus favus* suggests close affinites with Avalonia during the Llandeilian but does not resolve the absence of *Hammannaspis* in similar areas at that time. In the early Caradoc *Deanaspis* migrated into the basin from the east (Perunica). *Deanaspis* never dominated the Morrocan communities, unlike in Perunica. It is possible that *Onnia* first appeared in Morocco and soon extended its range into Perunica. By the mid Caradoc *Onnia* was the sole marrolithine in Morocco. The trinucleine, *Declivolithus*, extended its range from Perunica and Sardinia and replaced *Onnia ultima* for a short time during the late Streffordian.

6.3 Perunica

The Prague Basin was part of the microcontinent of Perunica that rifted from the Gondwanan margin during the Ordovician. Faunal evidence shows Perunica acted as a stepping stone between Baltica and Gondwana and, subsequently, Avalonia (Havlíček & Fatka 1992). Members of the Marrolithinae formed part of these faunal migrations during the Caradoc and Ashgill, reflecting Perunica's separation and movement into warmer lower latitudes.

The trinucleids of the Prague Basin have been extensively studied over the past 150 years and especially during the last sixty years. The large number of Bohemian species names has been reduced from 18 to 7, as workers have adopted a more population-based, and less typological, approach, see Přibyl & Vaněk (1969) and Shaw (1995).

6.3.1 Llanvirn

The oldest known marrolithinae from Perunica is a single poorly preserved specimen named *Marrolithus nefernofruaton* by Vaněk (1995) from the upper Dobrotiva Formation (uppermost Llandeilian). This specimen in all respects is similar to the Avalonian *Marrolithus favus favus* (Salter, 1847) and is synonymised with it. It shows the lateral fringe margin extension seen in the Avalonian material.

6.3.2 Caradoc

The lower-middle Caradoc, Letná Formation, is interpreted as a nearshore facies with storm deposits (Havlíček & Fatka 1992) and it is from within this environment that *Deanaspis goldfussii* (Barrande, 1846) was first described. Shaw (1995) correctly synonymised *D. senftenbergii* from the Vinice Formation, and *D. parviporus* from the Liben Formation with *D. goldfussii*. With the addition of these specimens *D. goldfussii* has now the longest stratigraphical range of all the Bohemian marrolithines, ranging from the base of the Aurelucian to the top of the Cheneyan (Liben to Vinice formations). The Nučice ore unit at the base of the Vinice Formations marks the end of the range of *D. goldfussii*. Snajdr (1981 named some Aurelucian, specimens from the Liben Formation as *Onnia linol*; Shaw (1995) assigned these to *Deanaspis*. The lower lamellae were poor and the specimens were older than any recorded *Onnia*. However, *Onnia etyma* sp. nov. from the Letna Formation has brought the range of *Onnia* down to the Lower Caradoc. Shaw (1995) wrongly syonymised *O. abducta* to the Avalonian *O. superba*. However, *O. abducta* shows a distinct sigmoidal outline to its pygidium. It is uncertain what advantage this particular shape conferred; the lower lamella does not appear different from species with the more usual arcuate margin.

Two species were assigned to *Marrolithus* by Přibyl & Vaněk (1969), *M. paulisper* and *M. ornatus* so extending the range of *Marrolithus* upwards considerably. Both are reassigned to a new genus, *Hammannaspis*, herein. *Hammannaspis? paulisper* (Přibyl & Vaněk, 1969) appeared in the Prague Basin in the Nučice ore unit and was replaced by *Deanaspis pongerardi* (Rouault, 1847), a wide ranging peri-Gondwana species, similar to *D. goldfussii* except for the much lower E_1 pit counts and less equal girder and first internal pseudogirder. *Hammannaspis ornata* occurs with *D. pongerardi* within the upper Caradoc Zahořany Formation in relatively deep basinal deposits laid down below storm wave base and

containing a low abundance shelly fauna (Shaw 1995). *H. ornata* was replaced by *Onnia ultima abducta* (Barrande, 1852) at the base of the Bohdalec Formation close to the peak of the volcanic activity. *O. u. abducta* ranged up through the poorly aerated pyritic deeper water claystones of the Bohdalec Formation.

6.3.3 Ashgill

The Králův Dvůr Formation corresponds approximately to the upper Pusgillian to upper Rawtheyan stages of the Ashgill. Its lower limit is not well correlated. *P. linearis*, which ranges from the upper Onnian to lower Pusgillian has not yet been found in Bohemia (Havlíček & Fatka 1992). The base of the Králův Dvůr Formation coincides with the sudden appearance of a new fauna, mostly immigrants from Avalonia and Baltica (Havlíček & Fatka 1992). It is in this formation that the last Marrolithinae in Perunica, *Onnia ultima ultima* appears over a short range.

6.3.4 Palaeogeography of Perunica

During the Llanvirn, Perunica lay on the Gondwanan margin east of Morocco, close to Armorica; rifting from the supercontinent sometime in the Aurelucian. The brief appearance of *Marrolithus favus favus* in the Llandeilian strongly suggests close association with Gondwnana margin where the species was widespread during that time, as well as being in Avalonia which was about the same latitude (around 60^0 S). It was immediately followed by the stratigraphically long ranging *Deanaspis goldfussii* which showed only slight geographical and temporal variation during the Caradoc, commonly associated with other *Deanaspis* (e.g. *D. vysocanensis*), other marrolithine genera (e.g. *Onnia*) or replaced for a time by *Hammannaspis paulisper*. Both *Onnia* and *Hammannaspis* were immigrants to Perunica from Morocco. *Deanaspis goldfussii* probably extended its range from Perunica to Sardinia and Turkey during the mid and late Caradoc.

6.4 Armorica

The shallow basinal area of Armorica was subjected to siltstone and sandstone deposition throughout the Ordovician, with only very little volcanic activity largely in the early Llanvirn (Henry 1989).

6.4.1 Caradoc

The middle Aurelucian part of the May Formation contains *Marrolithus favus favus* [= *M. bureaui* (Oehlert, 1895) of earlier authors] the only *Marrolithus* species found in the region.

The Burrellian *Deanaspis pongerardi* (Rouault, 1847) now includes the "*Onnia seunesi*" (Kerforne, 1900) and "*O. grenieri*" (Bergeron, 1894). The distinct girder and the first internal pseudogirder indicate the generic assignment, however the similar appearance of the upper lamellae to *Onnia* species has caused the earlier assignments to that genus. *D. pongerardi* shows variation in the presence or absence of an occipital spine but in all other respects the specimens are the same. *D. pongerardi* was originally created for a few specimens that showed bifurcating genal spines. Some specimens show the bifurcation is due to damage and subsequent repair. However, other specimens clearly show distinct bifurcation two-thirds down the genal spine, with the second spine invariably pointing inwards. Hughes in Owen 1985, p. 259 confirmed that the birfurcation was genuine. They remain to be examined in detail.

6.4.2 Armorican Palaeogeography

Armorica, like Iberia, Sardinia and Perunica, was part of the Gondwanan margin during the early Ordovician and all show close similarities in their Ordovician history; for example the Armorican Sandstone Formation is widespread across the four terranes. The complex relationship between Iberia, Armorica, Bohemia, Avalonia and Gondwana has recently been addressed by Gutierez-Marco *et al.* (1999) who used the diachronus arrival of certain faunal elements to postulate the relative positions of the micro plates. Christiansen and Stouge (1999) used a palaeo-oceanographical model to predict that the ocean current along the southern Gondwanan margin was anticlockwise during the Arenig; setting up a one-way route for migration from Iberia to Bohemia (see Text-Fig. 6.8).

By the early Caradoc, Armorica had rifted away from the Gondwanan margin (Henry 1989) and a basinal/open shelf environment developed. Henry (1989) showed bathymetric evidence from the palaeocommunities indicating an increased water depth from north to south and from west to east. The subsequent northward drift of the micro plate (from 70-75°S to approx. 50°S; Paris *et al.* (1999)) starved the area of significant siliciclastic sediment. Colonization by the marrolithines was sporadic and transient.

Marrolithus favus favus arrived in the Armorican Basin from Avalonia and remained only for a short period. Later, during the mid Caradoc *Deanaspis* migrated into the basin from either Perunica or Morocco.

6.5 Iberia

A single distorted upper lamella of a *Protolloydolithus* which is very similar to the type species, *P. ramsayi* but showing a higher degree of fringe pit organisation, has been recovered from the Valongo Formation, upper Llandeilian, northern Portugal. This is the only marrolithine known from northern Iberia. Lower Caradoc strata of central Portugal and Spain contain specimens of *Onnia ultima*.

6.5.1 Iberian palaeogeography

As noted above (6.4.3) the Iberian microplate had very close affinities to Armorica during the Ordovician. Brenchley *et al.* (1986) suggested that the Iberian platform had a water depth of about 80m during the Llandeilian/lower Velfreyan. Romano (1990) calculated a depth for northern Portugal of around 100-150m if a maximum average of 0.1° for the shelf slope was inferred.

6.6 Southern Sardinia

Three marrolithine species are known from Sardinia. *Deanaspis goldfussii fluminensis* is found in the Streffordian from near the top of the Monte Orri Formation to the middle of the Portixeddu Formation (Hammann & Leone 1997). It differs from the Bohemian *D. goldfussii goldfussii* by having the I_2 arc complete frontally. Hammann & Leone (1997) termed specimens from the upper Portixeddu Formation to *Deanaspis pongerardi* (Rouault, 1847). The contemporaneous species referred to by Hammann & Leone (1997) as *Deanaspis? novaresei* shows a sharp girder that is distinct along the entire fringe, with very little pseudogirder development, the upper lamella shows a distinct girder list external to it E_1 is tilted downwards and internal to it there is a concave curvature to the fringe. This is the only representative of the new genus *Hammannaspis* in Sardinia.

6.6.1 Sardinian palaeogeography

Sardinia, like Armorica, had a marginal setting through the early-mid Ordovician. Loi and Dabard (1999) proposed that Sardinia was geographically close to Armorica because of the presence of siliceous-argillaceous nodules in the Portixeddu and Postolonnec formations respectively. These storm deposited shelf mudstones and siltstone are directly above the widespread Armorican Sandstone Formation.

However, Sardinia was composed of two distinct basins with different sediment sources. The appearance of Baltic faunas in the basin filled with magmatic detrius and Gondwanan faunas (which included the marrolithines) in the terrigenous sediment basin was suggested by Loi and Dabard (1999) to show an almost equidistant position between Gondwana and Baltica in mid Caradoc times. Another possibility is that the Baltic faunas may have "preferred" one basin's sediments and Gondwana fauna preferred the other irrespective of their relative location between the two plates. The appearance of *Deanaspis goldfussii* in the late Caradoc, long after its early Caradoc origin in Perunica, could indicate that the environmental conditions preferred by tat species were not available in Sardinia until later or that there had been a rapid northward drift away from Perunica creating an oceanic barrier prevented *Deanaspis* extending its range to the smaller plates.

6.7 Turkey

Faunal evidence suggests that Turkey may comprise two or possibly three terranes originally arranged along the Gondwanan margin during the Ordovician (Dean *et al.* 2000; Dean & Monod 1990). The middle Caradoc Lower Shale Member of the Bedinan Formation from the northern Pontus and southern Taurus Mountain ranges contain all Turkish marrolithine species (Dean 1967, Dean 1983, Dean & Monod 1990 and Dean & Martin 1992).

6.7.1 Caradoc

The only marrolithine found in the Sosink, Şip Dere Inlier is *Hammannaspis orthogonia* (Dean, 1967) originally placed in *Marrolithoides* and later reassigned to *Deanaspis* by Hughes *et al.* (1975). It occurs in the Lower Shale Member of the Bedinan Formation but its precise chronostratigraphical horizon is not known.

Within the Bedinan Inlier to the east of the Şip Dere Inlier the species *Deanaspis g. goldfussii* [originally *Marrolithoides inferus* Dean, 1967] occurs, broadly contemporaneous with *H. orthogonia*. The previously termed *D. laticirrus* (Dean, 1967) is herein no more than a geographical varient of *Deanaspis g. goldfussii*.

The "mid third" of the Lower Shale Member contains *D. bedinanensis* (Dean, 1967). This is the last known marrolithine from the Caradoc of Turkey and is synonymous with *D. goldfussii goldfussii*.

6.7.2 Palaeogeography of Turkey

Turkey lay further along the Iapetan margin of Gondwana from the main area of marrolithine occupation (Text-Fig. 5.2). Throughout most of the Ordovician its latitude remained around 60° South. Its position is reflected by the late arrival of the marrolithines. The short duration and rapid turn over of *Hammanaspis orthogonia* and *Deanaspis goldfussii* subspecies suggests an opportunistic incursions. The widespread *Deanaspis goldfussii goldfussii*, replaced *Hammannaspis* and remained in the area for some time.

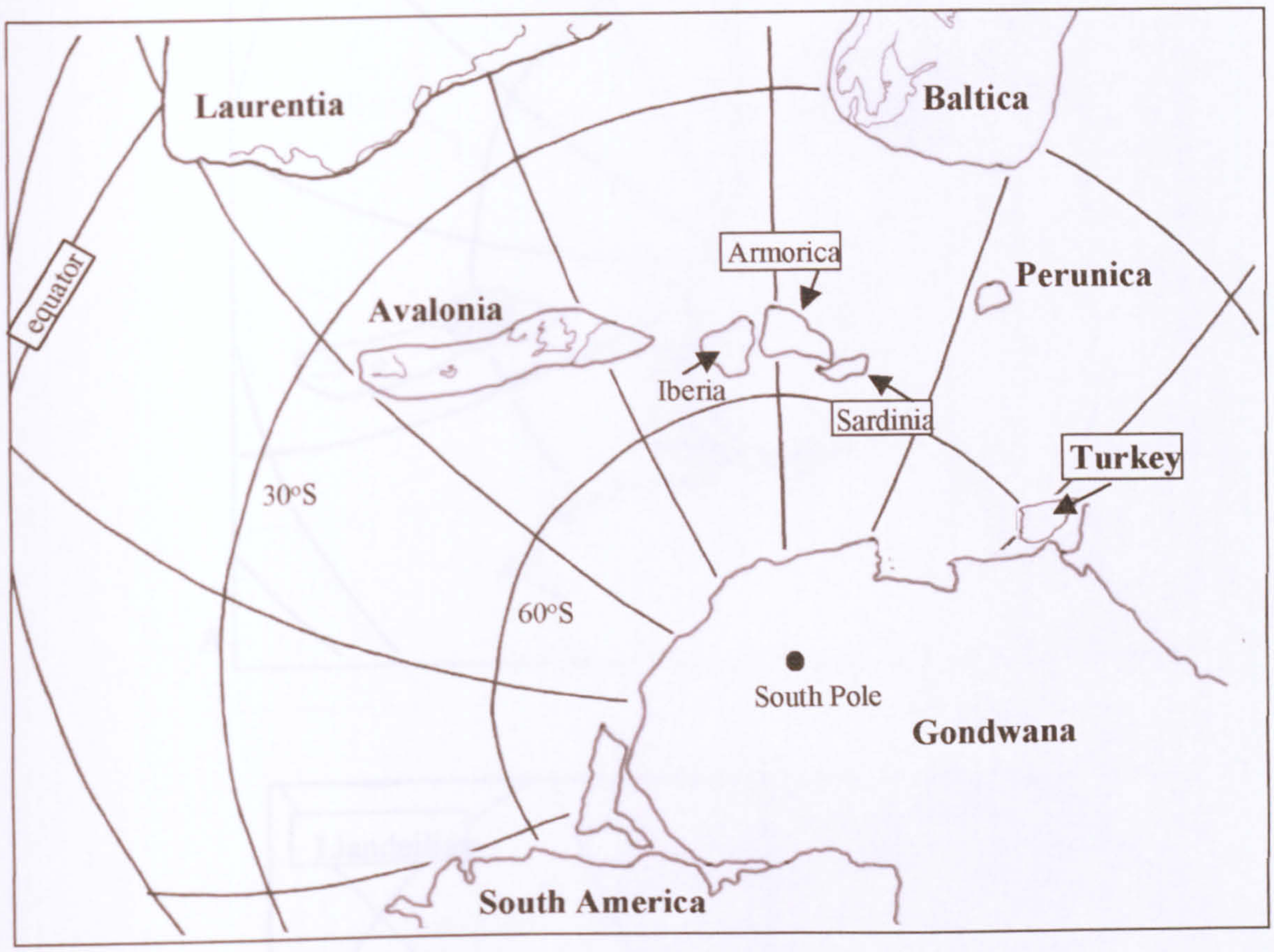
6.8 Venezuela

Cryptolithus terryi Leith, 1938, was placed in *Onnia* by Whittington (1954). Its age is still not known due to the lack of additional fauna but the morphology is very similar to *Reuscholithus reuschi* and is here placed in that species. The location of Venezuela in the mid Ordovician was at the same latitude as Avalonia (Cocks 1999) and hence had a similar ocean temperature, a possible environmental contstraint on the distribution of *Reuscholithus*. The position of South America has in the past been widely different but consensus now puts the part of the craton where Venezuela is situated now at high latitude. Although the stratigraphical evidence is lacking for the relative ages of the Venezuelan and Anglo-Welsh *Reuscholithus*, and hence the possible migration direction, the ocean circulation model of Cristiansen and Stouge (1999) suggested current flow would have been to be westwards along Gondwana's margin.

6.9 Uzebekistan

Deanaspis specimens from lower Caradoc strata indicates the range of the marrolithines extended further eastwards along the Gondwanan margin.

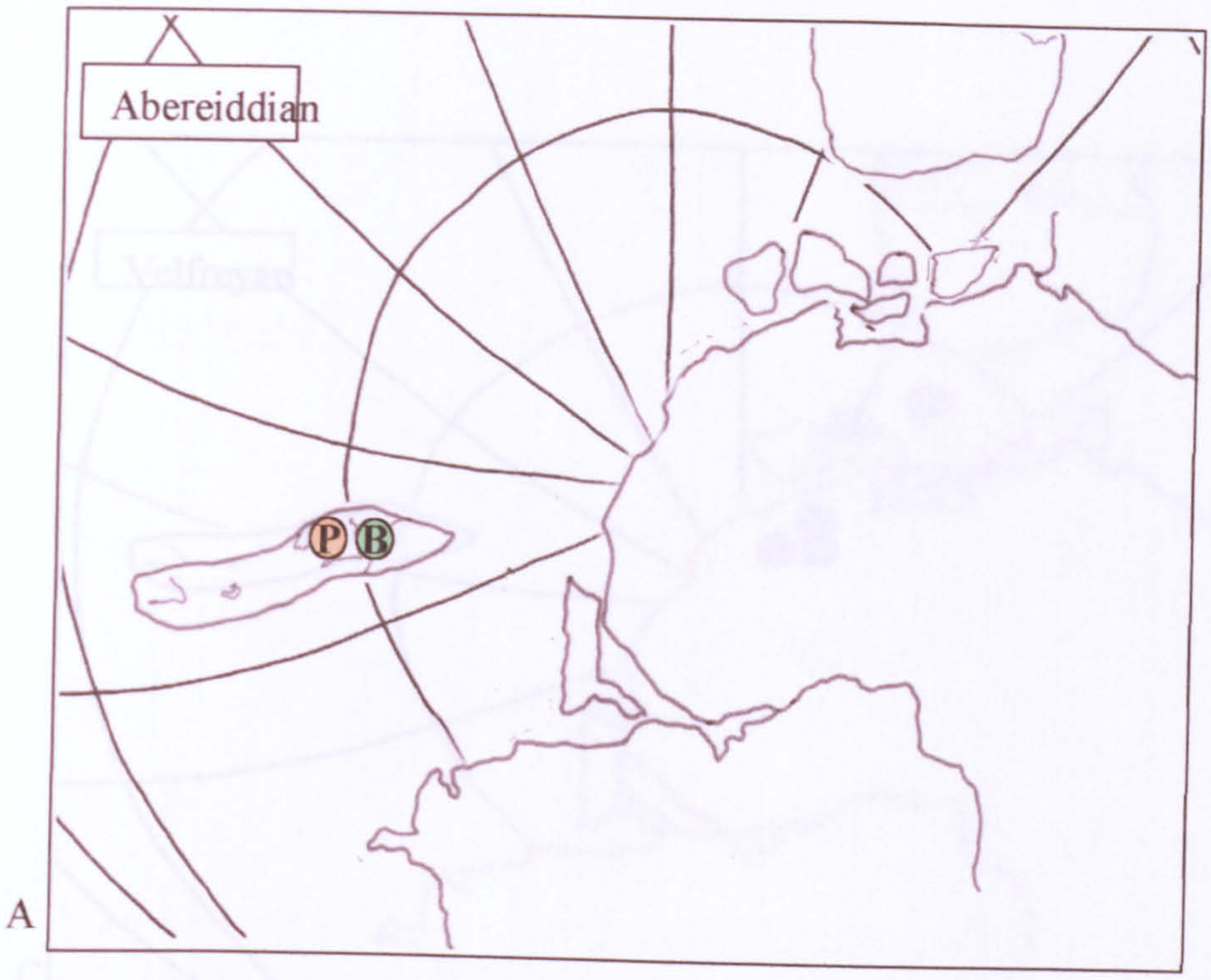
6.10 Migrations



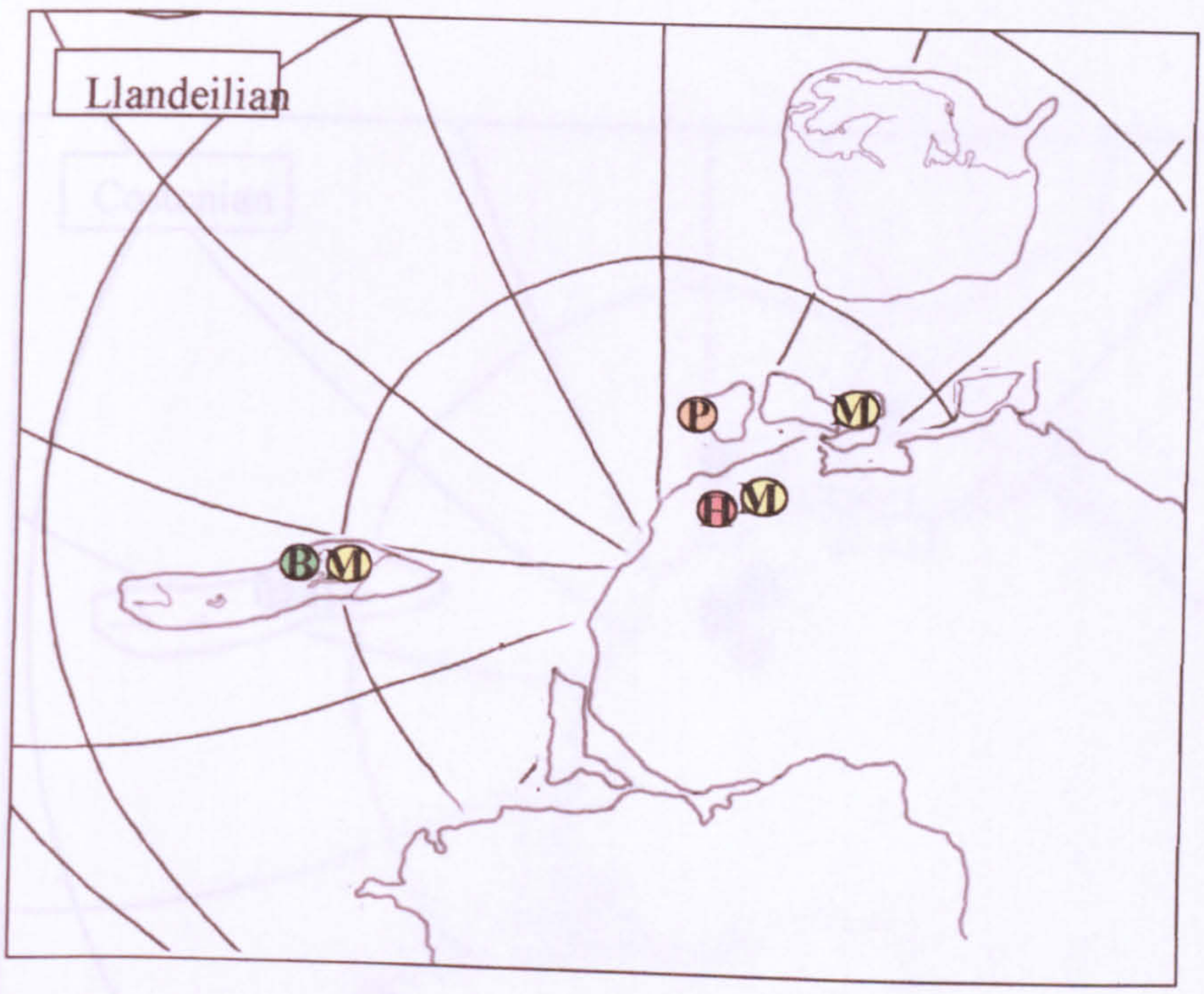
Key:

- (P) *Protolloydolithus*
- (B) *Bettonolithus, Whittardolithus* and *Lloydolithus*
- (M) *Marrolithus*
- (M) *Marrolithoides*
- (R) *Reuscholithus*
- (H) *Hammannaspis*
- (D) *Deanaspis*
- (O) *Onnia*

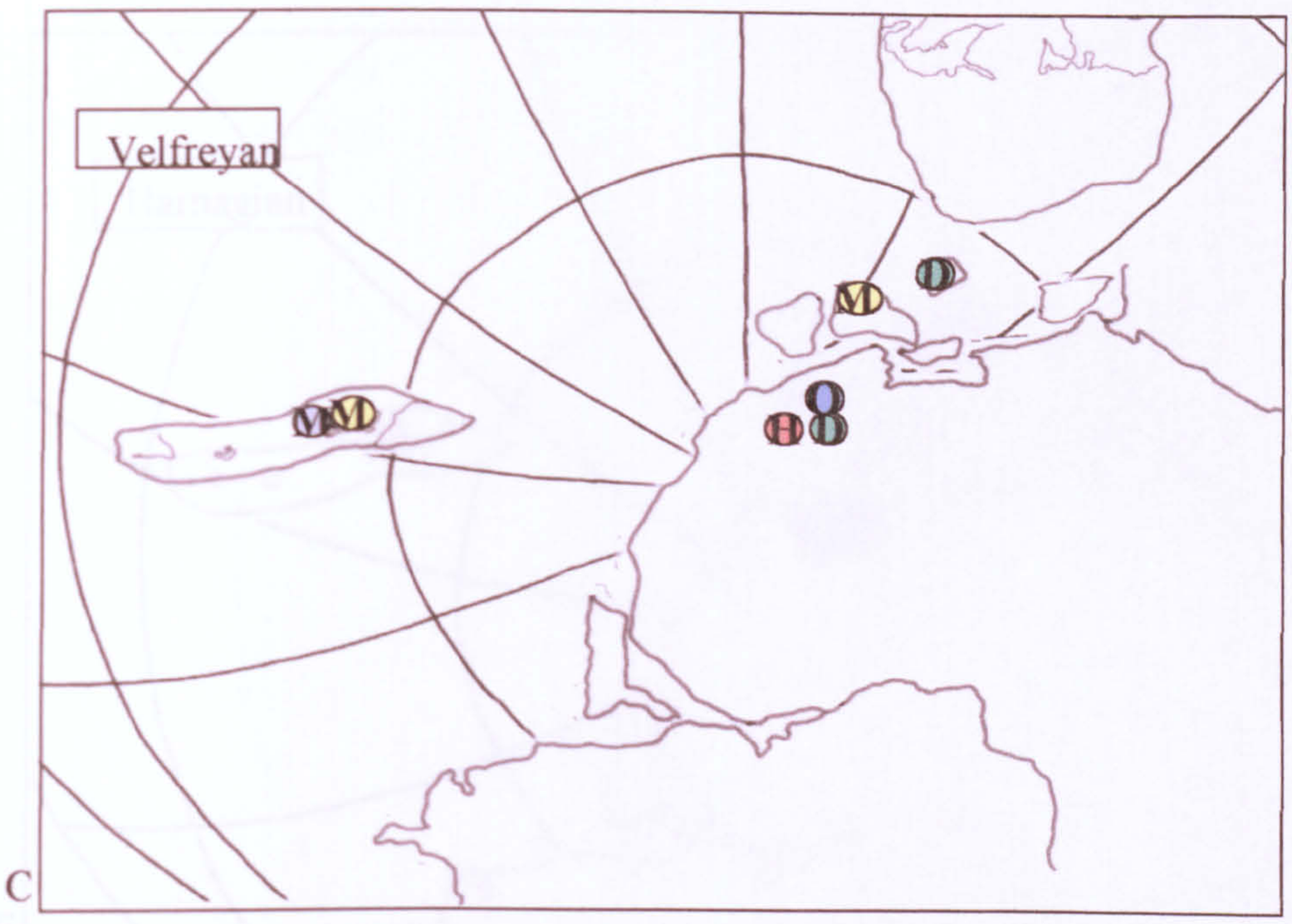
Text-Fig. 6.7. The following palaeogeographic reconstructions show the distribution of the Marrolithinae A-M.

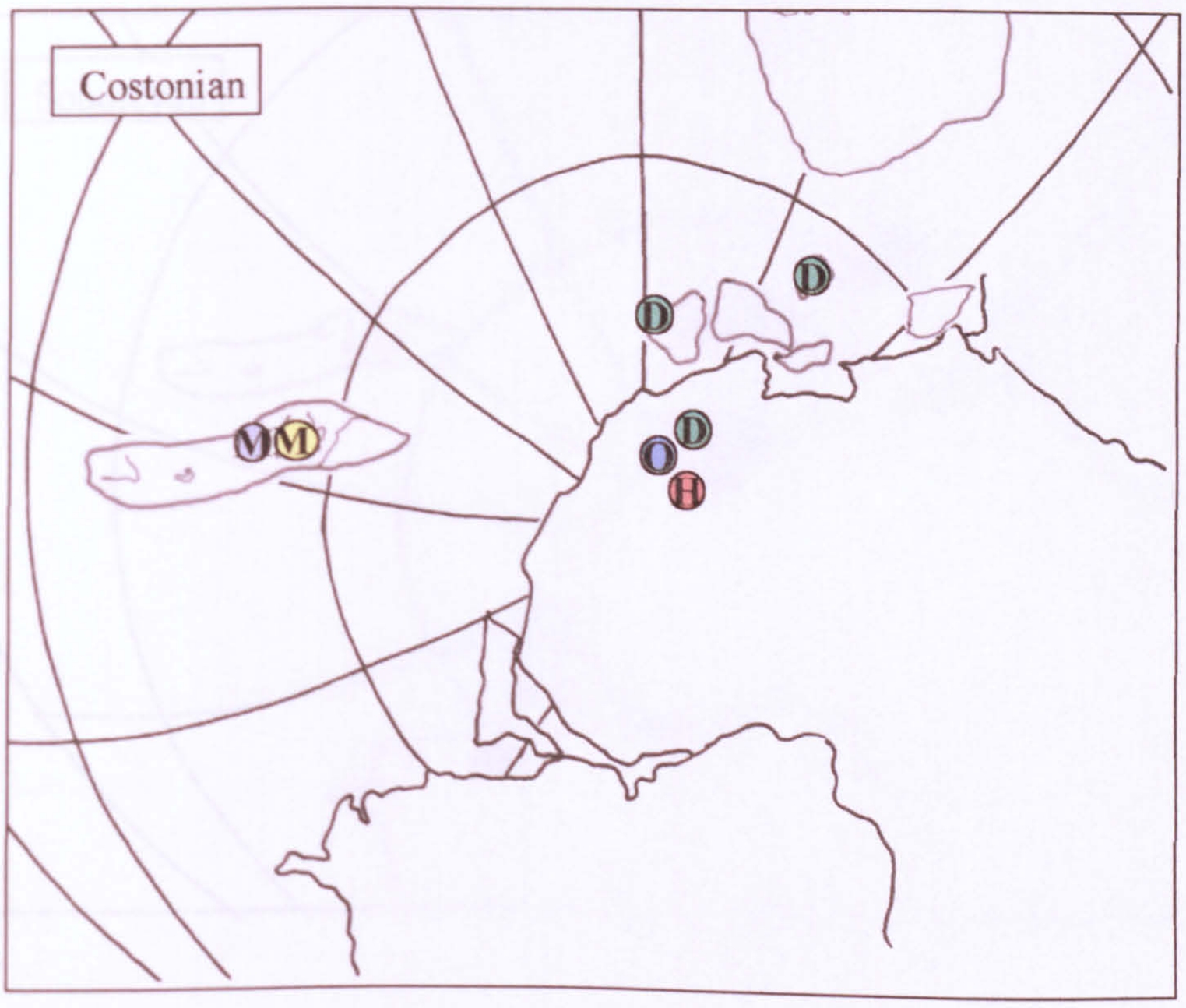


A

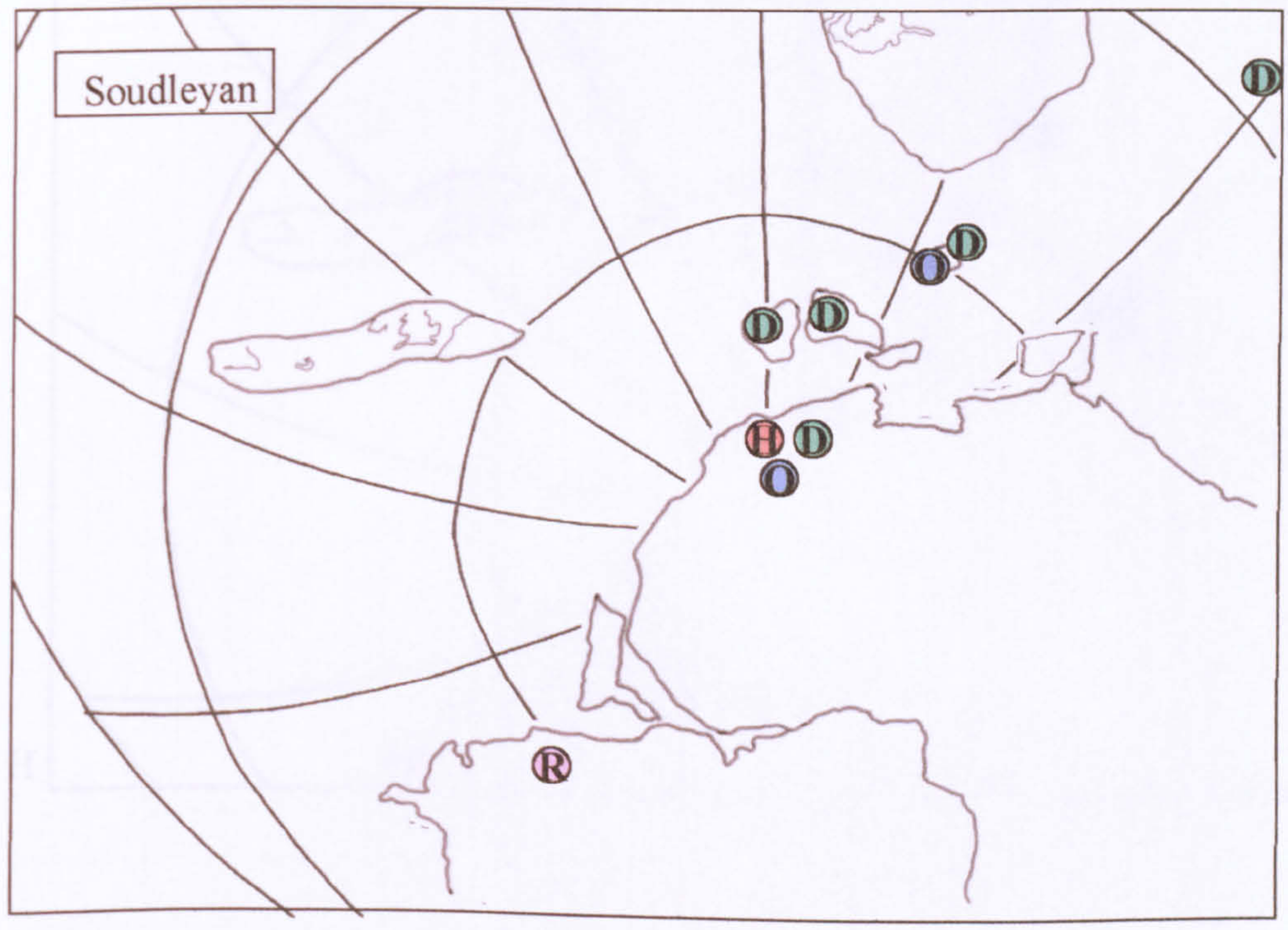


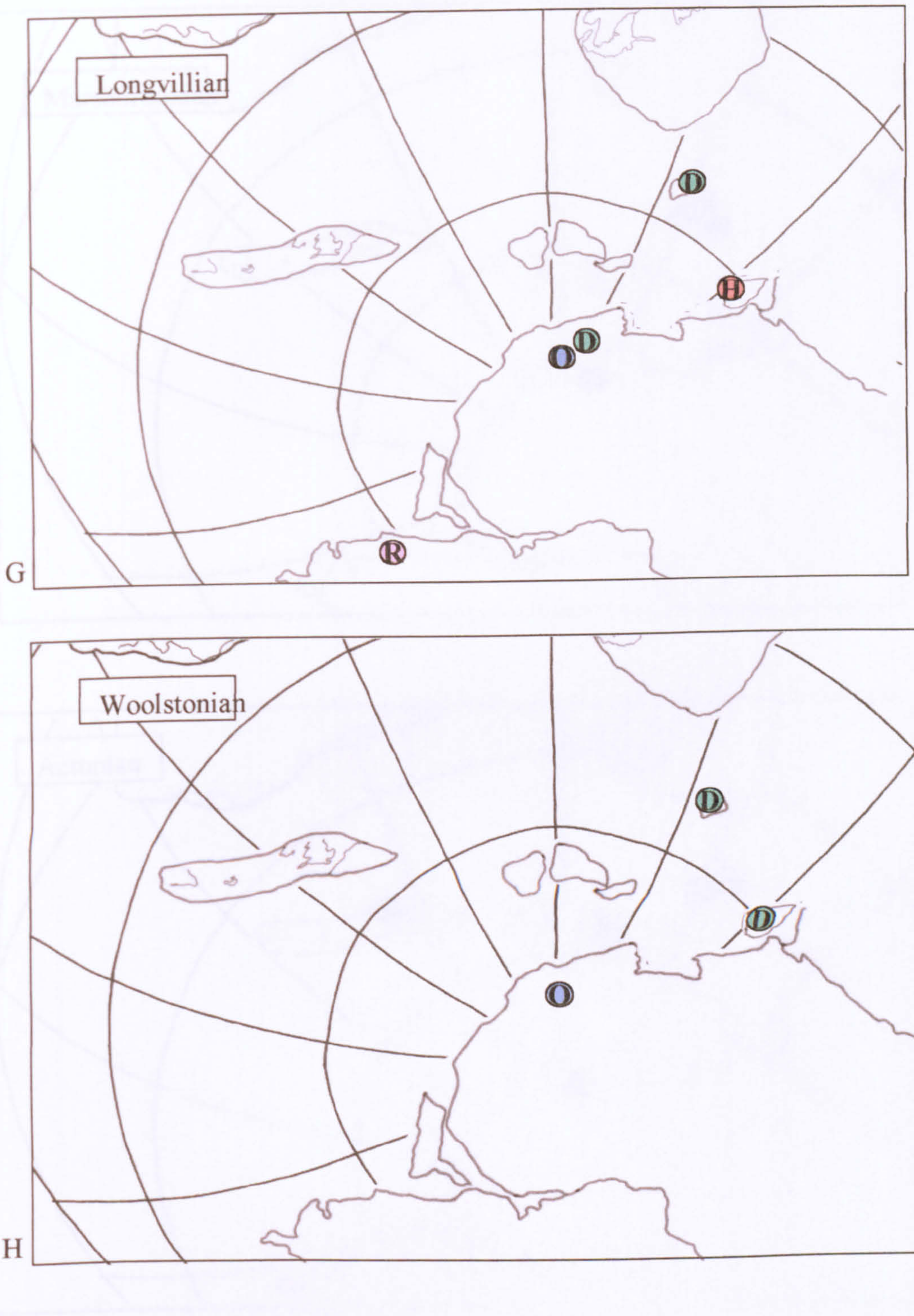
B

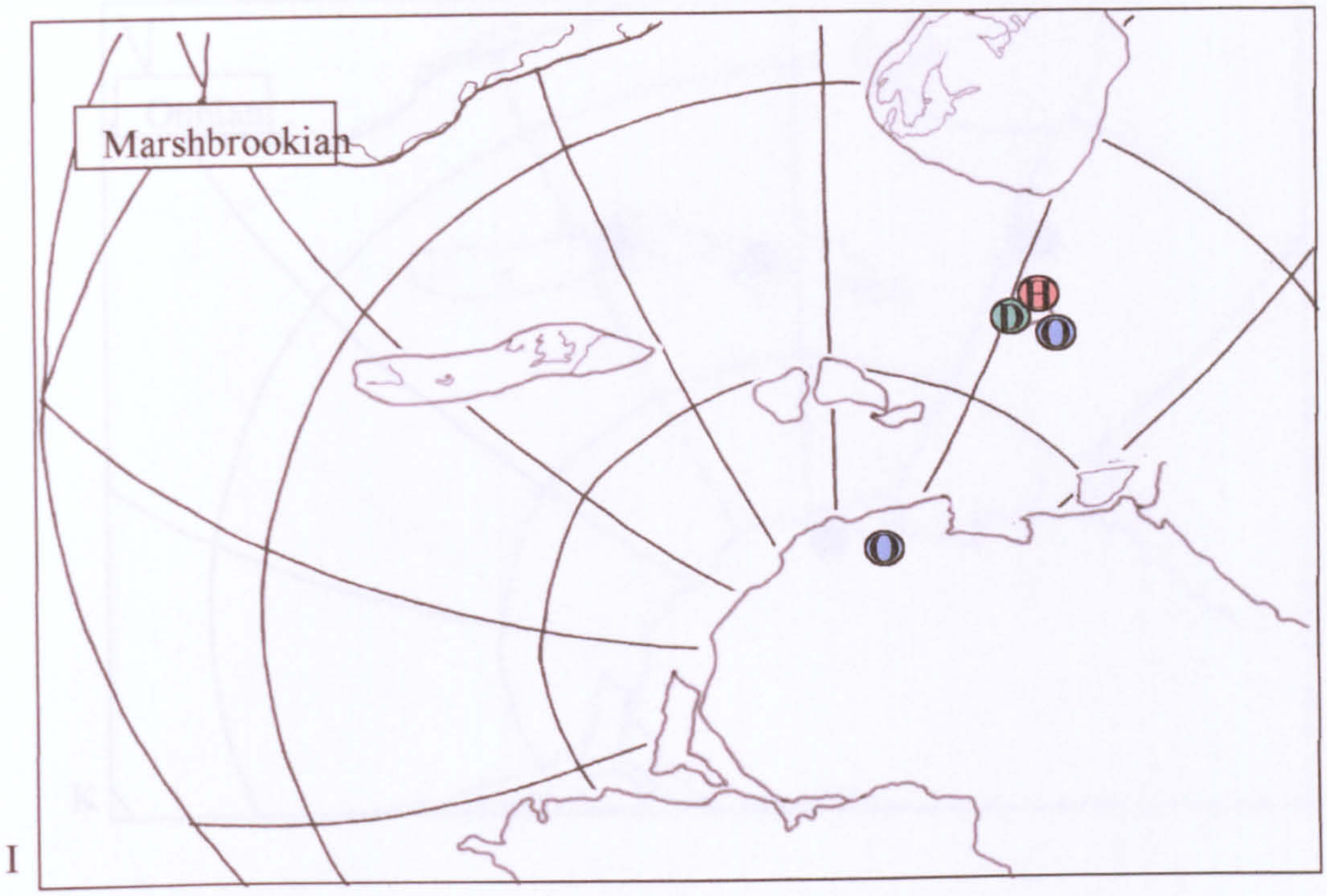

Velfreyan
C


Costonian
D

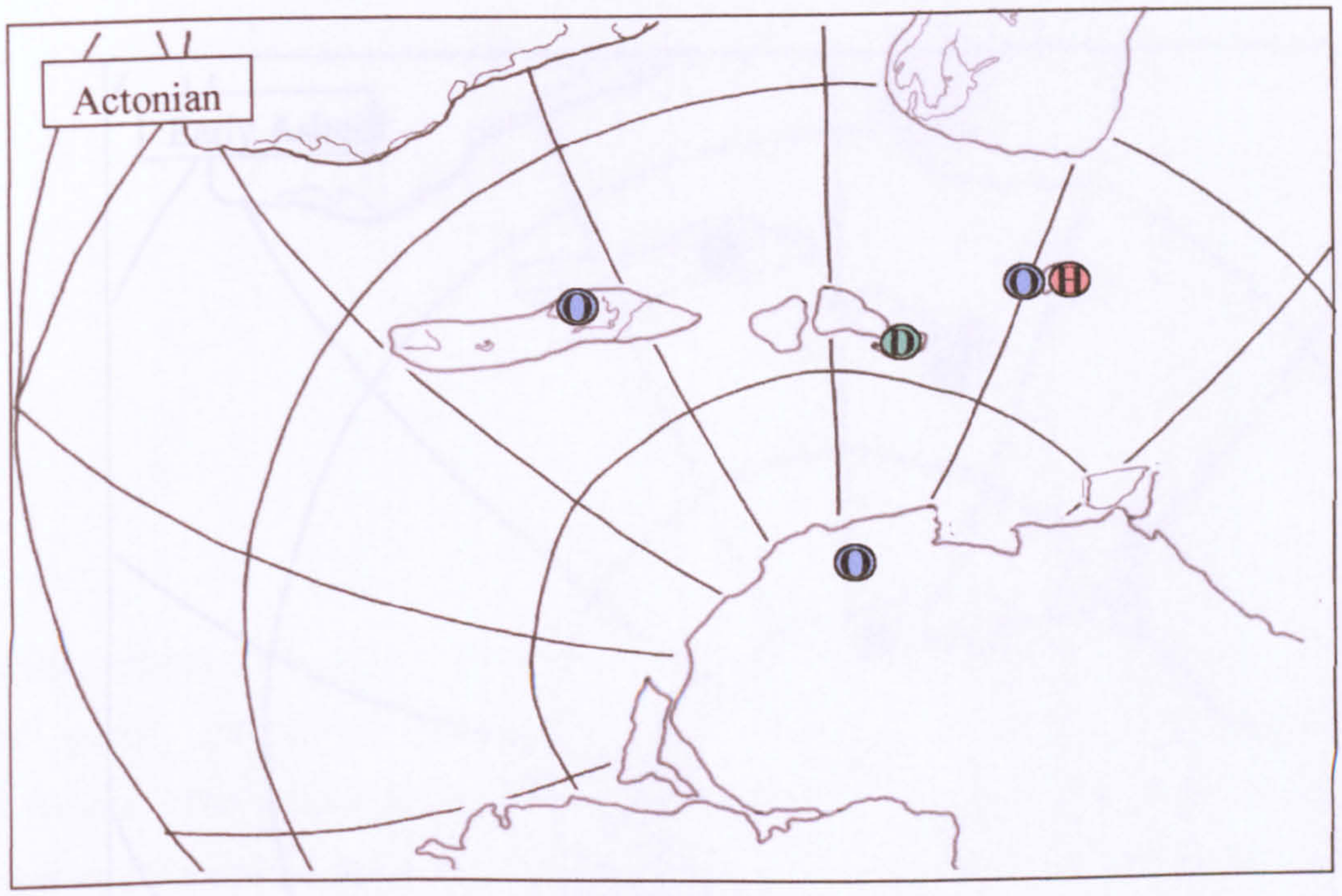

Harnagian
E


Soudleyan
F

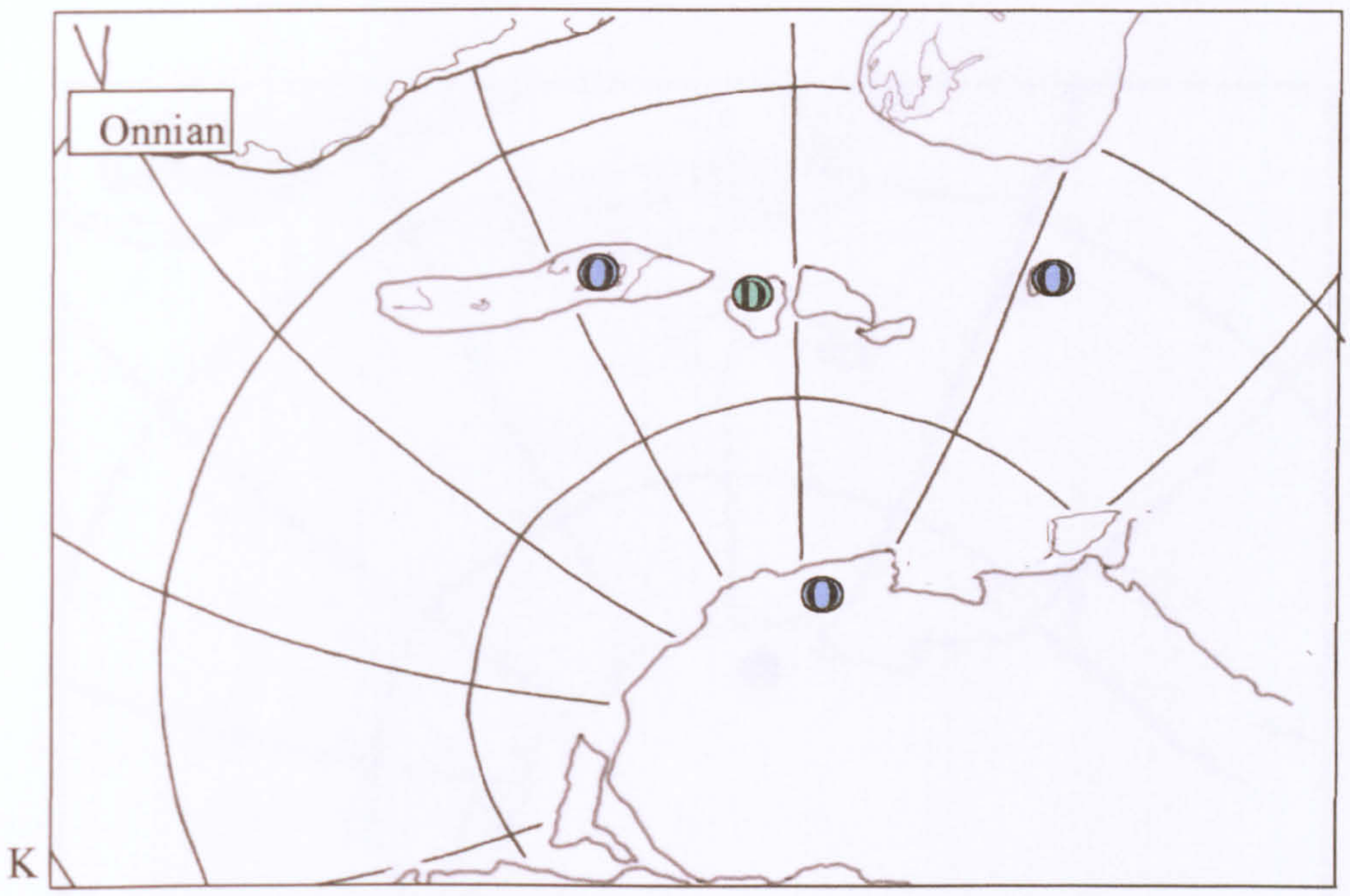

Longvillian
G
Woolstonian
H

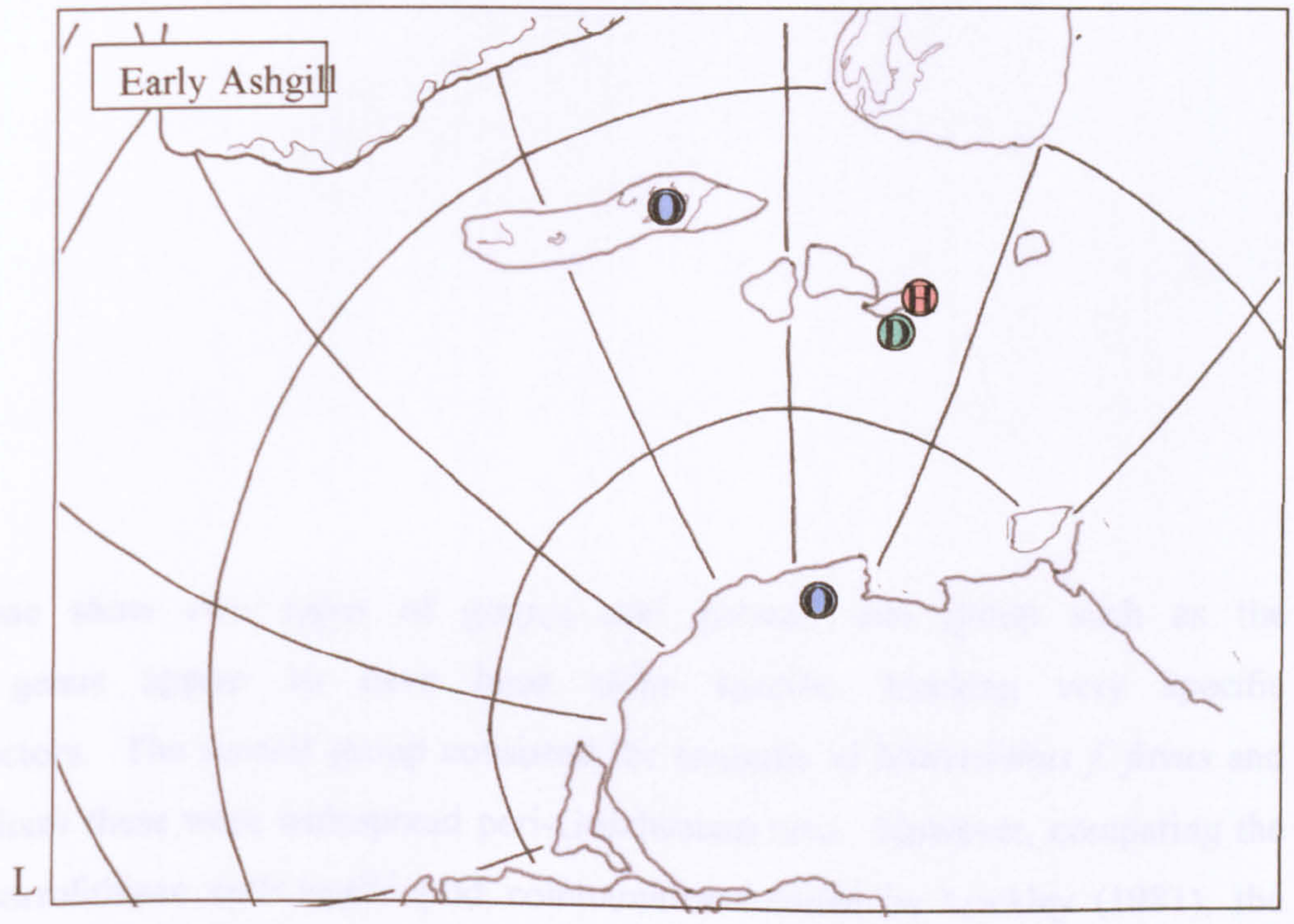


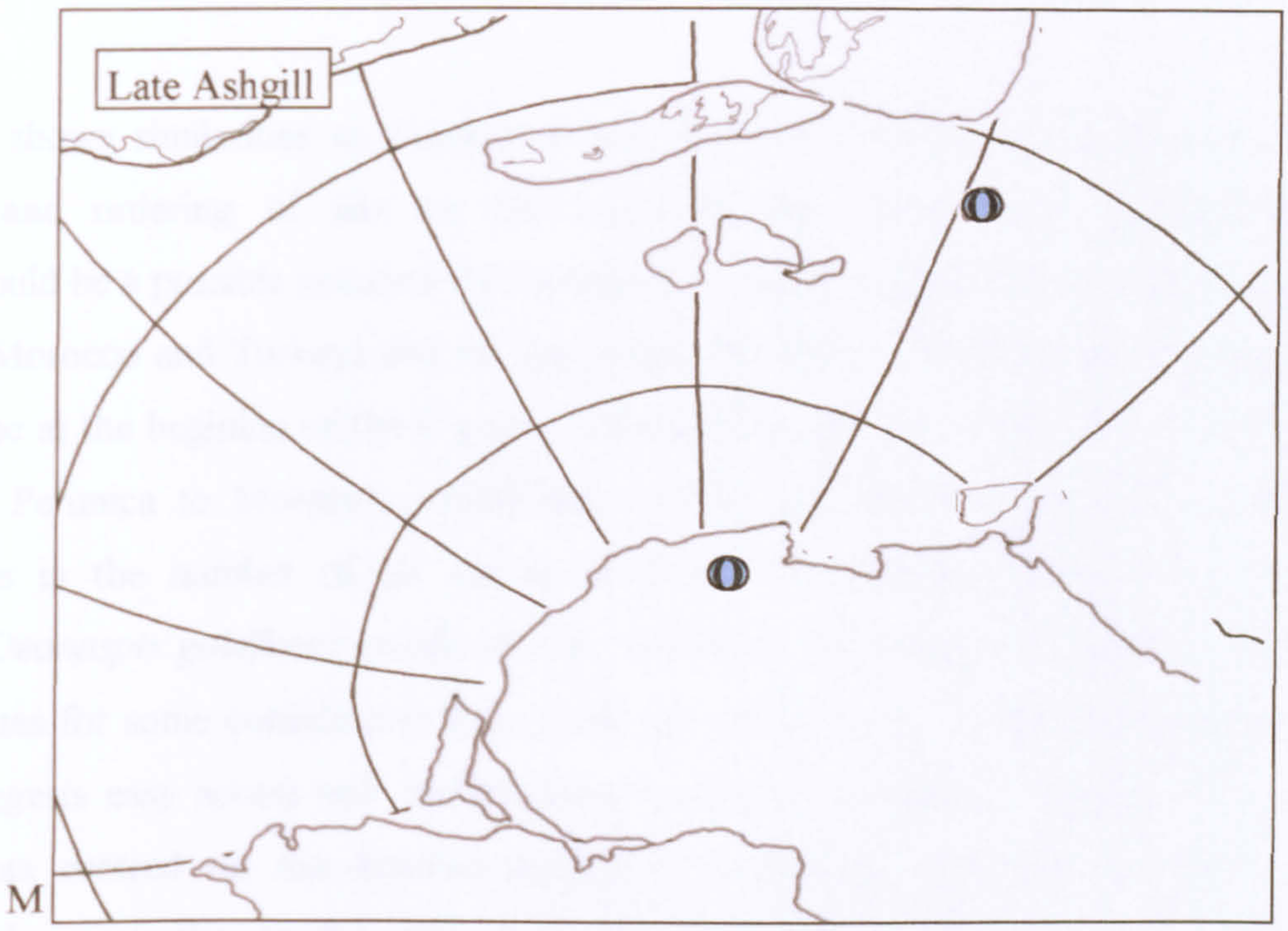
I



J


Onnian
K


Early Ashgill
L



The Marrolithinae show two types of genera and species, one group such as the *Marrolithoides* genus appear to have been niche specific, tracking very specific environmental factors. The second group consisted for example of *Marrolithus f. favus* and *Deanaspis goldfussii* these were widespread peri-Gondwanan taxa. However, comparing the ranges of the marrolithinae with brachiopod communities detailed by Lockley (1981), the trilobites were not community specific, crossing brachiopod boundaries spatially and temporly within the Anglo-Welsh Basin. Suggesting that the marrolithine populations were not constrained by the same ecological factors as those for brachiopods as the boundaries of each do not coincide. It has been long recognised that ecological generalists have greater

species longevity than ecological specialists (Kammer et al. 1997 and Sheldon 1990) and might suggest a possible reason for the stratigraphically and regionally long ranging *Deanaspis*.

Bettonolithus shows similarities to *Deanaspis* with its well defined pseudogirder on the lower lamella and ordering of pits on the upper lamella which might suggest that *Bettonolithus* could be a possible ancestor for *Deanaspis*, a genus distributed along the margin of Gondwana (Morocco and Turkey) and the microplate Perunica. By the onset of a global sea level increase at the begining of the Caradoc, *Deanaspis goldfussii* replaced *Marrolithus*, spreading from Perunica to Morocco, Uzbekistan, Turkey and Iberia (Text-fig 6.2 B-D). Slight variations in the number of pit counts or fringe pit elevation are seen in local populations of *Deanaspis goldfussii goldfussii* that dominated the Gondwana Iapetan margin and its microplates for some considerable time (early and mid Caradoc). The constistency of morphology suggests easy access and interbreeding between populations. Migration of the marrolithines was centred on the Iapetan margin of Gondwana, with the exception of Uzbekistan which was further to the east. These migration appears to have been strongly linked to ocean current directions, sea level changes and latitude.

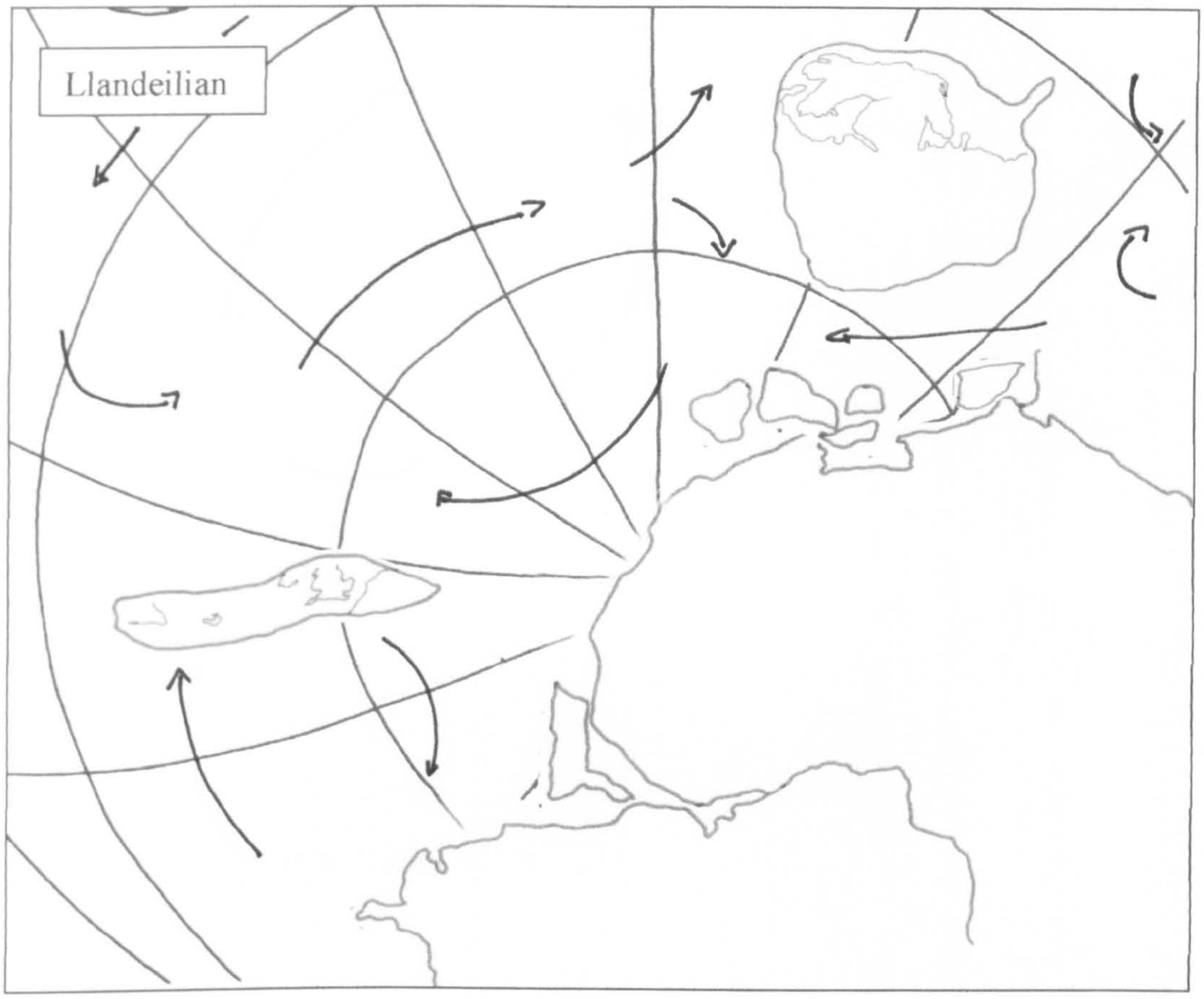
All migrations from Avalonia appear to have been in an easterly direction along the Iapetan margin. This is contrary to the Arenig palaeo-oceanic current model of Christiansen and Stouge (1999) see Text-Fig. 6.8. based on complex models of modern ocean currents, faunal distributions and lithology. Text fig 6.9, shows the ocean currents around the Iapetan ocean based on Christensen & Stouge (1999) superimposed onto the Llandeilian palaeogeography.

Text-fig 6.8. Christensen and Stouge (1999) Arenig palaeogeographical reconstruction showing trilobite distribution and ocean current directions.

The ontogeny of trinucleid trilobites included a planktonic phase (Chattertn and Speyer 1989). The suggestion of the ocean currents moving along the Iapetan margin from the east towards the west would suggest colonization westwards of the marrolithines. Migration from Avalonia towards Perunica would indicate movement eastwards. Clearly an anticlockwise gyre is needed in the Iapetan ocean close to the Gondwanan margin. This would not affect their overall scheme. See Text-Fig. 6.10.

The monospecific genus, *Reuscholithus* is only found in Avalonia and Venezuela. It is well constrained sratigraphically within the Anglo-Welsh Basin, but, its precise age in South America is unknown. Cocks (2000) placed both Avalonia and Venezuela near the same latitude during the early Caradoc. There are two possibilities for *Reuscholithus*, either it migrated from Avalonia to Venezuela, this would be consistent with the palaeocurrents of Christiansen and Stouge (1999) but contrary to the direction of migration of all other marrolithines, or it spread from Venezuela to Avalonia, in the same direction as other

migrations (Text-fig 6.9) but *Reuscholithus* appears to have strong ancestral links to Avalonia and so the latter suggestion should be discounted.



Text-fig 6.9. Christensen and Stouge (1999) ocean currents superimposed onto Llandeilian palaeogeography.

Text-fig 6.5 shows that the ocean currents east of Baltica may have assisted *Deanaspis* to get to Uzebekistan. The small channel between Baltica and Gondwana could have assisted in the isoaltion of Baltica from the Iapetan Gondwanan margin if the currents were sufficiently strong. As the distance between the two continents widened the currents may have reduced in strength but the width may have been sufficient to stop the pelagic young trinucleids. The clockwise gyre between Avalonia and South America would have aided the distribution of *Reuscholithus*. The major problem with this ocean current map is the clockwise gyre of the Iapetus Ocean. This direction along the coast is opposite to the major marrolithine migrations. Either the plates are in the wrong position or a smaller gyre is missing. The Iapetan gyre was based on the equatorial current and faunal distribution, a slight alteration to

the currents away from Baltica could produce a second gyre, in a west to east direction along the Gondwanan margin comensurate with the marrolithine migrations, see Text-fig. 6.10.

Text-fig. 6.10. The amended ocean currents.

In the late Caradoc *Onnia* extended its range northwards from Morocco and Perunica to Avalonia (Text-fig 6.2 K). The Marrolithinae persisted until the Ashgill in the deep basins of Perunica, Morocco and Avalonia, finally disappearing from them in the Cautleyan, possibly Cautleyan and Pusgillian respectively (Text-fig 6.2 L,M).

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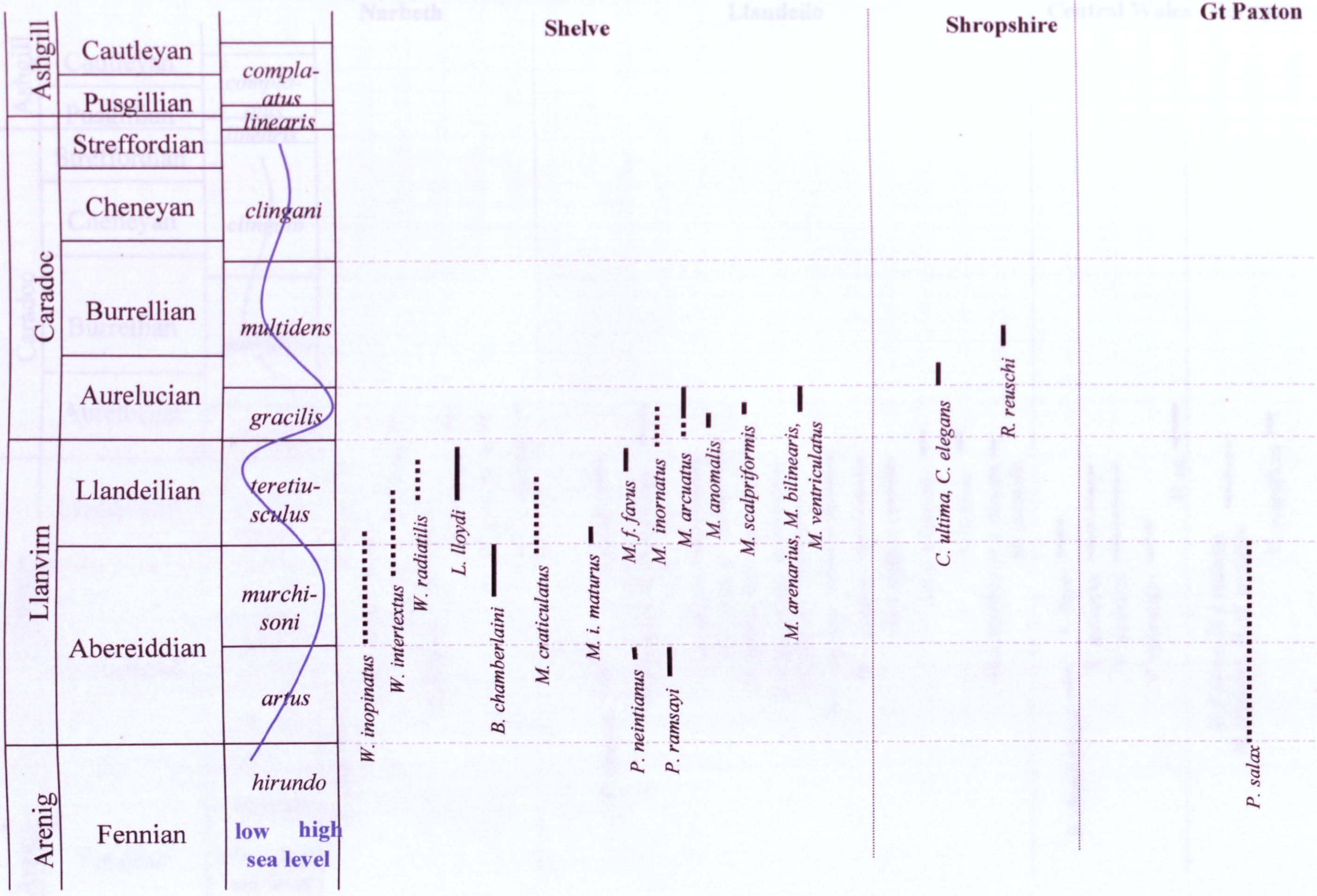
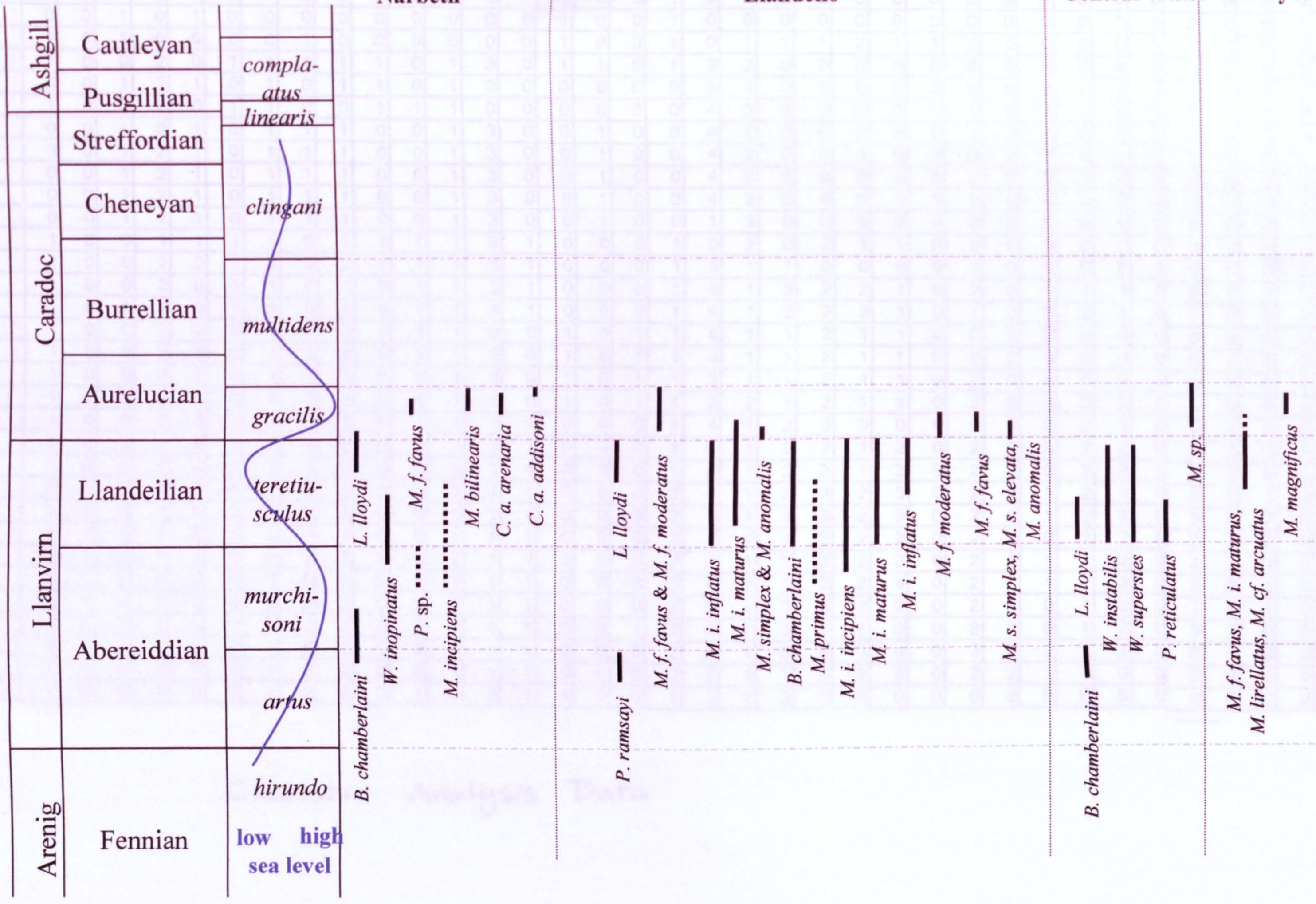
APPENDIX

Appendix. B. Range of Marrolithinae as previously understood within the Anglo-Welsh Basin. Local sea levels indicated.



Appendix. A. Range of Marrolithinae as previously understood within the Anglo-Welsh Basin. Local sea levels indicated.



species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38
Hanch-prim	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proto-nein	3	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Proto-rams	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proto-retic	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Proto-sala	3	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	1	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Betto-cham	1	0	0	2	0	1	1	1	1	1	0	1	3	0	1	1	0	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	0
Lloyd-lloy	0	0	1	2	1	0	1	0	1	1	0	1	0	0	0	0	0	0	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Reusc-reus	1	0	0	2	0	1	1	0	0	1	1	1	0	0	0	0	0	0	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0
Whitt-inop	0	0	1	2	1	0	1	1	1	0	0	1	3	0	0	1	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Whitt-inst	0	0	1	2	1	0	1	1	1	0	0	1	3	0	0	1	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Whitt-inte	0	0	1	2	1	0	1	1	1	0	0	1	3	0	0	1	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Whitt-radi	0	0	1	2	1	0	1	1	1	0	0	1	3	0	0	1	0	0	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Whitt-supe	0	0	1	2	1	0	1	1	1	0	0	1	3	0	0	1	0	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Costo-eleg	1	0	0	1	1	1	1	0	1	1	1	1	3	1	0	0	0	1	5	2	0	2	1	1	0	2	0	0	0	0	0	0	0	0	0	3	3	0
Costo-ulti	1	0	0	1	0	1	1	0	2	1	1	1	3	1	0	0	0	1	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	0
Costo-aren	1	0	0	2	0	1	1	0	1	0	1	1	3	1	0	0	0	1	4	1	3	2	2	1	0	2	0	0	1	1	0	2	0	0	0	3	3	0
Cost-a-add	1	0	0	2	0	1	1	0	1	0	1	1	3	1	0	0	0	1	4	1	3	2	3	1	0	1	0	0	2	1	0	1	0	0	0	3	3	0
Mides-anom	1	0	0	2	0	0	1	0	2	0	1	1	3	0	1	0	1	1	4	1	1	2	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0
Mides-arcu	1	0	0	2	0	0	1	0	2	0	1	1	3	0	1	0	1	1	4	1	1	2	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0
Mide-s-ele	1	0	0	2	0	0	1	0	2	0	1	1	3	0	1	0	1	1	3	1	1	2	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0
Mides-simp	1	0	0	2	0	0	1	0	2	0	1	1	3	0	1	0	1	1	3	2	1	2	1	1	0	2	0	0	0	0	0	0	0	0	0	1	0	0
Marro-aren	1	0	0	1	0	1	1	0	2	0	1	1	3	1	0	0	0	1	4	1	2	3	0	0	0	0	0	0	2	2	0	2	2	0	0	3	3	0
Marro-bili	1	0	0	1	0	1	1	0	2	0	1	1	3	1	0	0	0	1	4	1	3	3	1	2	0	2	2	0	2	2	0	2	2	0	0	3	3	0
Marro-crat	1	0	0	1	0	1	1	0	2	0	0	0	1	1	0	0	0	1	4	1	3	3	1	3	0	2	2	0	2	3	1	2	2	0	0	3	0	0
Marro-favu	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	4	1	3	3	2	3	0	2	2	1	2	3	0	3	2	1	0	3	3	0
Marr-f-mod	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	4	1	3	3	2	3	0	2	2	1	2	3	0	3	3	2	0	3	3	0
Marro-infl	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	4	1	3	3	2	2	0	2	2	0	2	2	0	2	2	0	0	3	3	0
Marr-i-inc	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	4	1	3	3	2	3	0	2	2	1	2	2	0	2	2	0	0	3	3	0
Marr-i-mat	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	4	1	3	3	2	4	0	2	2	1	2	3	0	2	2	1	0	3	3	0
Marro-inor	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	5	1	3	3	2	2	0	2	2	0	1	3	0	2	2	1	0	3	0	0
Marro-lire	1	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	1	2	4	1	3	3	1	2	0	2	2	0	1	2	0	3	2	0	0	3	3	0
Marro-magn	2	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	5	1	3	3	3	4	0	3	2	2	3	2	0	0	0	0	0	3	3	0
Marro-prim	1	1	0	1	0	0	1	0	2	0	0	1	1	1	0	0	0	2	5	1	1	3	2	3	0	2	2	1	0	0	0	0	0	0	0	3	3	0
Onnia-grac	1	0	0	1	0	0	1	0	2	0	1	1	3	1	1	1	0	1	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1	0

Cladistic Analysis Data

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